A REEVALUATION OF SEED PLANT PHYLOGENY[1]

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ABSTRACT

Seed plant phylogeny is evaluated using a data set of 46 terminals (taxa) and 103 morphological and anatomical characters. Cladistic analyses using the criterion of parsimony were performed on the complete data set as well as on subsets of the data, e.g., excluding fossils and/or combining various complex taxa into single terminals. The results support the placement of the cycads as the sister group of a monophyletic group that includes several fossil "seed ferns" as well as extant *Ginkgo*, conifers, gnetopsids, and angiosperms. When fossils were included, Bennettitales (cycadeoids) were part of an "anthophyte" clade that included gnetopsids and angiosperms. *Pentoxylon* was a sister taxon to the core anthophyte clade, in some, but not all, of the most parsimonious trees. *Caytonia* was not found to be closely associated with the anthophyte clade, but instead was often associated as a sister taxon of the glossopterids, and these two taxa were consistently outside of the *Ginkgo*–conifer–anthophyte clade. In all most parsimonious trees for all analyses, *Ephedra* was to the outside of a clade that included all angiosperm taxa, *Gnetum*, and *Welwitschia*, thus rendering the traditional gnetopsid clade paraphyletic. New information is provided on the morphology of *Caytonia* and some previous interpretations of homology of the caytonian "cupule" are rejected. The effects of sampling, compartmentalization, and polymorphism are explored in these data, showing how different results may be obtained when polymorphic or "summary" terminals are used. The need for more work on gnetopsids and fossil taxa is suggested.

INTRODUCTION

In recent years, several phylogenetic analyses of seed plants have been published, some with explicit emphasis on the relationship of angiosperms to other seed plants (Hill & Crane, 1982; Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992; Loconte & Stevenson, 1990). We refer the reader to Loconte & Stevenson (1990) for a summary and comparison of the results of several of these studies. In this paper we present a new cladistic analysis of seed plant phylogeny based on morphological characters. Unlike the Loconte and Stevenson analysis, our analyses include several fossil taxa as terminals, as did the analyses by Crane (1985) and Doyle & Donoghue (e.g., 1986a, b, 1987).

This study encompasses two major goals. The first, and most obvious, is to provide a character analysis of seed plants, followed by a cladistic analysis and a phylogenetic interpretation of those results. While we feel that we have provided some new insights, a few new characters, and what we feel are more neutral codings (i.e., fewer phylogenetic hypotheses encoded) of some previously used characters, we fully expect readers to focus most intently on the topologies of the cladograms that we present. While this is understandable, our position is that at present all seed plant analyses, whether they are morphological or molecular, are highly preliminary, and suffer from numerous problems. Thus, the second, and we feel most important goal of this paper, is to discuss and evaluate the numerous problems encountered in such broad analyses, show the effects of some of these problems, and propose some solutions, or at least partial solutions, to some problems. However, the overriding message that we wish to convey is that most of the problems associated with such analyses have not been adequately dealt with to this point. The solutions to problems associated with large-scale analyses of diverse taxa may require additional theoretical advances as well as vast improvements in computer hardware and software capabilities. In particular, the inability to analyze efficiently data sets that are larger than a few score taxa forces users to "compartmentalize" analyses, which may result in solutions that are not globally parsimonious (Nixon & Carpenter, in press).

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Materials and Methods

Sampling

Fossil taxa were selected for inclusion on the basis of availability of published or original data, and whether or not we had confidence in proposed reconstructions based on separate fossil organs. Wherever possible, we checked characters as used in previous analyses against original descriptions and revisions in the literature, and in some cases we reinvestigated fossil morphology when material was available (e.g., *Caytonia*, some bennettitalean taxa). These investigations resulted in differences in some character codings relative to previous studies. These differences are discussed below in the section describing fossils, and in Appendix A, which treats all characters used in the analyses.

Extant taxa were sampled to ensure representation of major seed plant groups. Within angiosperms, taxa were selected to represent broad variation and to ensure representative sampling of groups that have previously been hypothesized to be morphologically similar to hypothetical primitive angiosperms. For example, *Magnolia* (Magnoliaceae) represents the traditional Besseyan view (Bessey, 1897) of the primitive angiosperm, *Ceratophyllum* (Ceratophyllaceae) the first branch in various morphological (Les, 1988) and *rbc*L analyses, and *Chloranthus* (Chloranthaceae), *Piper* (Piperaceae), and the monocots the possible basal groups (e.g., Burger, 1977, 1981). The "Amentiferae," considered basal in the "Englerian" view, were represented by *Chrysolepis* (Fagaceae), *Betula* (Betulaceae), and *Casuarina* (Casuarinaceae). *Drimys* (Winteraceae) represents the modified Besseyan hypothesis of Cronquist (e.g., 1981) and others, and *Calycanthus* (Calycanthaceae) the "first branch" of the morphological analyses of Loconte & Stevenson (1991). Other angiosperm taxa were included in an effort to represent major groups and provide connecting structure among the other terminals; e.g., *Platanus* and *Hamamelis*, based on previous analyses, appear to be reasonably placed between the "higher hamamelids" (Fagaceae, Betulaceae, Casuarinaceae in our analyses; see Nixon, 1989) and the lower hamamelids (e.g., *Trochodendron*, *Tetracentron*) and magnoliids. Because we wanted to combine our data with existing *rbc*L data in a separate project (Albert et al., 1994), sampling decisions were further restricted a priori by the availability of *rbc*L data for taxa in our analyses.

The "complete" data set included all taxa (46 terminals) and characters (103) as presented in Table 1. Following the convention of Henning86, characters are numbered starting with character 0. The majority of characters (80) were binary; of the remaining 23 multistate characters, 15 were treated as nonadditive (unordered) and eight were treated as additive (ordered), as discussed in Appendix A.

In addition to the complete data set, several modified data sets were also constructed and analyzed. These included data sets that had certain terminals or groups of terminals excluded completely, and/or groups of terminals "condensed" into single terminals. Terminal condensations were automatically generated in the matrix editor DADA (DADA386 ver. 0.87, Nixon, 1993b). The "strict" condensation option of DADA was selected, in which the new generated "condensed" terminal was scored as polymorphic (*) for all characters that would be polymorphic (variable within the original terminals within the group). DADA translates polymorphic cells to ambiguous (−) upon submission to the Hennig86 daughter process, but retains the polymorphic coding (*) in the working matrix. Terminal exclusions were also automated through the DADA-Henning86 interface, assuring accuracy by retaining a single master copy of the complete data matrix.

The data sets generated by the above procedures included numerous combinations that we are not reporting here because of space limitations. The results that we report here are based on the following five matrices:

I. Complete analysis: 46 taxa, 103 characters; 23.61% ambiguous, of which 1.36 are polymorphic (ambiguity 17.51% excluding 11 within-angiosperm characters, 92–102).

II. Fossils excluded: 31 taxa, 97 characters; 12.31% ambiguous, of which 0.32% are polymorphic (ambiguity 7.69% excluding 11 angiosperm characters, 92–102).

III. Single angiosperm terminal: 29 taxa, 83 characters; 21.77% ambiguous, of which 1.93% are polymorphic.

IV. Fossils excluded, single angiosperm terminal: 14 taxa, 66 characters; 6.61% ambiguous, of which are 3.59% polymorphic.

V. Fossils excluded, single angiosperm and conifer terminal: 9 taxa, 57 characters; 17.8% ambiguous, of which 1.54% are polymorphic.

Note that the number of informative characters for reduced data sets varies. No characters were removed or recoded other than for the condensed terminals. Differences in number of characters used reflects the reduced variation when taxa are removed and/or condensed. Thus, some characters are excluded that vary only among terminals that

TABLE 1. Data matrix. Characters 0–59. ? = unknown; – = inapplicable; . = uncertain homology; * = polymorphism. All treated as missing data.

```
                    0    5    10   15   20   25   30   35   40   45   50   55
                    |    |    |    |    |    |    |    |    |    |    |    |
Aneurophyton        000?010001000-???0000??0?0-0-*0???00?00-00?0000-0-?-?--0?---
Archaeopteris       000?110011210-???000000000-0-0000?0010002000000-0-000--0?-?-
Lyginopteris        0.0?110000210-???000000011110000000?000.100000-0-000--0????
Medullosaceae       0.0?210000210-???200000011110*000000???0.101010-0-000--0????
Callistophyton      010?100000210-???10000001.11000?00000000103101110-10000--0011?
Corystosperm        01??120001200-???10100001011000000?001000300l110-11000--0????
Lepidopteris        ???????????????-???10?0???*111000?0?001000300l110-0-000--0????
Tatarina            011??????????-???10?00??0111000?0?00?00?30?1110-?????--2????
Glossopterids       010-130101200-???100000000111010?0000.*00.0?1110-110??--2????
Caytonia            ???????????????-????00?0??0.-101010?001000311l110-11000--0????
Williamsoniella     010??????????-????00000?0111000001?1.01102101110-0-1?1100????
Cycadeoidea         010?100100110-???200000111110000l?1.01102101110-0-111100????
Williamsonia        010?100100110-???200000111110000l?0.01102101110-0-1?11?0????
Pentoxylon          011?230011200-???000000001110000-000.00.0001110-0-.00--0????
Cordaites           011?110111200-???100000000-0-00000001000001l011-10000--00???
Cycadaceae          0000221100210-000200000011110000000010003001110-0-000--00010
Stangeriaceae       0000121100110-000200001011110000000010003101110-0-000--00010
Zamiaceae           0000-21100110-00020000.011110*00000010003101110-0-000--00010
Ginkgo              0110130111200-000100000100-0-00000001001311lll0-0-000--00010
Taxaceae            0110110111200-000?01000102-0--00000010003010111-0-100--00110
Taxod Cupress       0110110111200-000201*00102-0--0000001*003110111-0-100--00110
Araucariaceae       0110110111200-000201*0010*-0-00000001000301011l-0-100--00110
Pinaceae            0110110111200--00201000102-0--0000001001301.111-*0000--00110
Cephalotaxaceae     0110110111200-000201000102-0--00000010003010111-0-000--00110
Podocarpaceae       0110110111200-00020100010*-0-00000001001301.111-*0000--00110
Ephedra             0201130111211000100011010l-0--00000.01113101100-0-1011110100
Welwitschia         0201130111211000120011010101l100112.01110101110-0-1011111101
Gnetum              0211120111211000120011010112l100112.11110100100-0-1011001101
Chloranthus         .10113010-1111011110111101121111110101-1111201*0-0-1110102101
Piper               .10112010-1111011110010101221101101011011120110-0-1110002101
Winteraceae         0101140101110-0111100001011211011111110011120110-0-1110102101
Calycanthus         0201130101211111111010010112110110111001112lll0-0-1110002101
Eupomatia           0101120101111111111000010112110110111001212lll0-0-1111002101
Magnolia            0101120101111111111000110112110111111001212lll0-0-1111002101
Persea              0101130101211111111000010112110111111?101.120100-0-11.-002101
Nymphaea            210112010---0-0110100111012211011111l001212lll0-0-1111002101
Lilium              110112010---11111000.10101021101101111011121110-0-1110102101
Dillenia            0101120101111l?1100000010112110110111101120l2000-1110102101
Caltha              110112010-1111011000010101221101101111011201200O-1110102101
Trochodendron       0101120101110-0111100001011211111l1.1001112012000-1110102101
Platanus            0101120101211101100000110122110110211101112012000-1110102101
Hamamelis           0101140101211101100000110112110110111111212012000-1110102101
Chrysolepis         0101140101201101100000110112110110211111212012010-1110102101
Betula              0101140101211101100000110112110110211111212012020-1110002101
Casuarina           0101140101211101100011010210--0110001--1212012020-1110002101
Ceratophyllum       210101010---0-011000100100-0-00--0011001112010O-0-11.--02101
```

TABLE 1. Continued. Characters 60–102.

	60 65 70 75 80 85 90 95 100
Aneurophyton	?----00----------0-00?-0----------
Archaeopteris	?00--00----------?000-00?-0----------
Lyginopteris	?000-0111000010000100100000??0?----------
Medullosaceae	?000-0111000-10100110100?000????----------
Callistophyton	?000-02110000?-1101001?0?000????----------
Corystosperm	?110002200 10?0-1100000?1???????----------
Lepidopteris	?1?0-022?010?0-1100000?0???????----------
Tatarina	?1?0-022101 0?0-1100000?0???????----------
Glossopterids	?1?0-022*000?0-1000001?0??00????----------
Caytonia	?1?0-02210?0?0-1000001?1???????----------
Williamsoniella	?1?0-0100010?101000?00?1???????----------
Cycadeoidea	?1.0-0100010?10100000011?0???1??----------
Williamsonia	?1?0-0100010?10100000?1?0?????----------
Pentoxylon	?1?0-0200000?0-1001001?1???????----------
Cordaites	?11100200.00?0-110100??0?000????----------
Cycadaceae	0000-0?1100000-1001100100000000----------
Stangeriaceae	0100-011000100-1001110100000000----------
Zamiaceae	0100-011000100-1001110100000000----------
Ginkgo	0100-02.000000-1101000100000000----------
Taxaceae	11?0-020000000-1100001000000101----------
Taxod Cupress	1111?020*00000-1100001000000101----------
Araucariaceae	1111102001 0000-1110001000000101----------
Pinaceae	1111102001 0000-1110001000000101----------
Cephalotaxaceae	1110002000 0000-1101000100000101----------
Podocarpaceae	111000200-0000-1101000100000101----------
Ephedra	1110001000101111100000110000010 1----------
Welwitschia	1110001000101111010000211111111 1----------
Gnetum	1110001000101111000000211111111 1----------
Chloranthus	11.0-12.000011020000011101101 10?.--111-1101
Piper	11.0-12.000011020000011111101 10?0--10113112
Winteraceae	11.0-12.110011020000011101101 1010000111-000
Calycanthus	11.0-12.010011020000011101101 1011000110-000
Eupomatia	11.0-12.110011020000011101101 1011.00110-000
Magnolia	11.0-12.010011020010011101101 1010000110-000
Persea	11.0-12.010011020000011101101 100001101-3101
Nymphaea	11.0-12.110010020000011101101 1000000110-000
Lilium	11.0-12.110011020000011111101 1000011001 3110
Dillenia	11.0-12.*000110200000111011011000010011-000
Caltha	11.0-12.010011020000011101101 1000010010-000
Trochodendron	11.0-12.110011020000011101101 10010-0011-010
Platanus	11.0-12.000011020000011101101 1000100114101
Hamamelis	11.0-12.010011020000011101101 1011100112121
Chrysolepis	11.0-12.010011020000011101101 1001111001 3121
Betula	11.0-12.010010020000011101101 1011100012121
Casuarina	11.0-12.010011020000011101101 101.--000121-1
Ceratophyllum	11.0-12.000010?200000111011011 00011011-1100

are excluded in the condensed analyses. For example, characters that are relevant only within-angiosperms (92–102) were operationally excluded from analyses in which angiosperm taxa were condensed into a single terminal.

Additionally, as reported elsewhere (Albert et al., 1994), the complete morphological data set was combined with *rbc*L sequence data. For those analyses, fossil taxa were scored as ambiguous (missing) for all *rbc*L data.

Cladistic analyses were performed on Intel 486 IBM PC compatibles using Hennig86 version 1.5 (Farris, 1988), run as a 16-bit DOS daughter process of DADA386 ver. 0.87. All modified data sets were generated directly within DADA, ensuring that characters were scored identically in all separate analyses. Alternative character optimizations and trees for publication were produced using Clados ver. 1.4 (Nixon, 1993a).

In order to increase the likelihood of finding a complete set of most parsimonious trees (Mickevich & Farris, 1982; Luckow & Pimentel, 1985), taxon order in the larger data sets was pseudorandomly shuffled 100 times using the "autospin" option of DADA (Nixon, 1993b) and directly submitted to Hennig86 using the "mh*" option. Trees were collected from each run, and the final set was analyzed with heuristic branch swapping ("bb*"). The autospin command of DADA automatically removes redundant trees from replicate runs by filtering tree files through the Hennig86 "xsteps u" option. This provides an accurate count of the number of trees found, and allows generation of a consensus tree from all the unique trees generated by replicate runs.

Some of the data sets that were generated by condensing groups had few enough terminals to allow analysis by the "ie*" ("implicit enumeration") option in Hennig86, which guarantees to find the complete set of most parsimonious trees for the data. For these data sets (IV, V), replicate randomized taxon order was unnecessary.

Two non-seed-plant fossils (*Aneurophyton*, *Archaeopteris*) were included in the full data matrix, and trees were rooted between *Aneurophyton* and the remainder of taxa. All analyses were simultaneous (outgroups included without a priori assumptions about topology Farris, 1972, 1982; Clark & Curran, 1986; Meacham, 1984, 1986; Nixon & Carpenter, in press). Because outgroups were treated like all other taxa in the analysis, cladograms were globally most parsimonious for the entire dataset (outgroup + ingroup). The final cladograms were rooted between the outgroup terminals and ingroup. In analyses that excluded fossil terminals, trees were rooted between cycads and the remainder of the extant seed plants, based on the results of the full analyses and previously published analyses (Loconte & Stevenson, 1990). It should be noted that such rootings do not affect the topologies of the trees reported.

Theoretical Considerations

Missing Data

Problems associated with missing data and/or polymorphism have not been discussed extensively in the literature, but interest in this topic has increased in recent years (e.g., Nixon & Davis, 1991). We prefer to separate the concept of missing data from that of missing values or general ambiguity. The former occurs when data are unknown or not collected, and the latter when a cell is scored as a "missing" value for reasons other than missing data, such as uncertain homology or polymorphism. Most currently available computer programs, including Hennig86 (Farris, 1988), PAUP (Swofford, 1991), NONA (Goloboff, 1993), MacClade (Maddison & Maddison, 1992) and Clados (Nixon, 1993a), treat missing data computationally the same during optimization and calculation of tree length, e.g., as if the missing cell had all possible states present. Some programs that search for most parsimonious cladograms (e.g., PAUP and NONA) allow the coding of subset polymorphism (e.g., states 0 and 2 present, but not state 1), while polymorphism must be coded as ambiguous (missing), or equivalent to all states present, in the current version of Hennig86. Although Nixon & Davis (1991) discussed the problem in the context of polymorphism coded as missing data (e.g., for Hennig86), these problems are *not* solved by subset polymorphism coding as is available in PAUP and NONA. Other problems do occur, and it is possible that when polymorphic terminals possess only a subset of possible states, PAUP and Hennig86 may report different tree lengths for the same topology; thus, extensive and correlated polymorphism may not allow Hennig86 to find the most parsimonious trees. However, when such conditions exist, the problems pointed out by Nixon & Davis (1991) are most likely even more severe than the problems associated with coding subset polymorphism as missing, and it is doubtful whether the results of either program would be stable to further analyses of monothetic subgroups of polymorphic taxa. The best solution to this problem is to avoid complex multistate characters and polymorphic terminals as much as possible.

Although it is obvious that high proportions of

missing data introduce uncertainty into analyses, it is not yet clear whether this uncertainty is predictable, how to measure it, or how much missing data is allowable within a particular analysis before the results should be rejected as unreliable. This topic is presently the subject of experimental investigation (Nixon, in prep.). Preliminary results indicate a predictable interaction of missing data and homoplasy; the effect of missing data is accentuated by high levels of homoplasy. Data sets that include numerous fossil taxa often have high levels of missing data as a result of imperfectly preserved fossil organs and the difficulty in determining homology of characters that cannot be investigated equally in all terminals. Thus, recent analyses of seed plant relationships have suffered from high levels of missing data, often in excess of 20% of the total number of cells (e.g., 24% in Doyle & Donoghue, 1986b; 23.6% in our complete analysis, or 17.5% excluding inapplicable states coded as ambiguous for some within-angiosperm characters). In our analyses, the vast majority of cells scored as missing were due to lack of information for fossil taxa; this is reflected in the much lower levels of ambiguous data when fossils were excluded from the analyses. Polymorphism in our analyses was low, ranging from 0.3 to 3.59% of the cells in the various matrices. The highest levels were in those matrices with condensed terminals, because condensations generate polymorphism for each character that varies among the condensed terminals.

COMPARTMENTALIZATION, ARTIFICIAL TERMINALS AND POLYMORPHISM

One of the most serious problems in previous analyses of seed plants has been the treatment of complex, diverse groups as single terminals, which then presents difficulty when these terminals are polymorphic (variable within the group as a whole) for certain characters used in the analysis. Coding terminals as polymorphic or ambiguous for these characters may result in incorrect tree topologies, as pointed out by Nixon & Davis (1991). In some cases, cladograms found when terminals are scored as polymorphic do not include any of the most parsimonious cladograms found when the terminal is subdivided into monomorphic units. The method of coding diverse terminals as single units is in effect "compartmentalization" and constraint of the data (see Maddison et al., 1984). This method of compartmentalization relaxes the application of global parsimony, which accounts for the disparate results obtained when analyses are run simultaneously versus compartmentalized and/or constrained. We present some examples of this problem using various modifications of our seed plant matrices below. Contrary to popular belief, this is a problem whether computer programs accept polymorphic codings or whether polymorphisms must be coded as ambiguous. Wherever possible, we have reduced polymorphism in our data by breaking terminals into units that are monomorphic for each character (Nixon & Davis, 1991).

Compartmentalization may result in equally serious errors, which are more subject to researcher bias, when polymorphic terminals are not coded as polymorphic or ambiguous, but instead are coded as having the "presumed" plesiomorphic state for the group represented by the terminal. In the Doyle & Donoghue (1986a, b, 1987) analyses, angiosperms and some other diverse groups, such as conifers and cycads, were treated as single terminals, and several characters were scored either as polymorphic (in those cases missing because of the computer programs used) or as the presumed primitive state for all angiosperms. Thus, for example, the "angiosperm" terminal in the above analyses was scored as having alternate leaves, bitegmic anatropous ovules, and spirally arranged microsporophylls (= stamens), under the assumption that these states were primitive in angiosperms. On the other hand, other polymorphic characters of angiosperms were scored as missing, or ambiguous, such as presence of vessels. Given these choices in character coding, it is not surprising that the Doyle & Donoghue (1986a, b, 1987) analyses did not find a close relationship of angiosperms to Gnetales (with opposite leaves, single integuments, orthotropous ovules, whorled microsporophylls, and foraminate- or simple-plated vessel elements). In order to avoid such bias, we have sampled several angiosperm taxa for observed characters, instead of presuming an angiosperm ancestral form that predisposes placement of angiosperms in our cladograms. Of course, such an approach has other problems, mostly due to potential undersampling (see Nixon & Wheeler, 1991), but we consider these problems to produce less bias than does the practice of designating ancestral states for polymorphic terminals.

HOMOLOGY DECISIONS

One of the most serious problems in any broad cladistic analysis of higher level taxa is the problem of homology assessment among highly divergent taxa. Typically, the more closely related taxa are, the easier such assessments of homology may be.

Seed plant analyses of necessity include taxa with disparate morphology of reproductive and vegetative structures. Some uncertainty exists in homology assignment for some taxa for almost every character in the analysis. For instance, whether angiosperm flowers are compound strobili, and whether carpels are "megasporophylls" are just a few of the problems encountered in an analysis of seed plants. In order to avoid decisions that are laden with phylogenetic hypotheses, we have attempted to code characters based as much as possible on direct observation of features. Whether or not we have succeeded or failed in this effort will be left to the judgment of the reader, and undoubtedly some will vehemently argue that complex models *should be* incorporated into the analysis. An example of such a complex model used by previous authors is the "cupule" of *Caytonia*, which has been coded as homologous with the second integument of angiosperms and Bennettitales by some previous authors (Crane, 1985; Doyle & Donoghue, 1986a, b, 1987). We discuss our interpretation of this structure, both in terms of coding and in terms of our cladistic results, in greater detail below.

Included Taxa

See Table 1 for a list of taxa and the complete data matrix.

FOSSIL TAXA

Fossil taxa were selected for inclusion in our analyses on the basis of availability of data, i.e., completeness of fossils or presumed reconstructions, and relevance to the problem of seed plant phylogeny. While numerous angiosperm fossils are now known, relatively few are complete enough or different enough from modern taxa to be relevant in a broad seed plant analysis (see Crepet et al., 1991, for a review of fossil flowers). Thus, we have not included any angiosperm fossils in our analyses. The descriptions of key fossil taxa below are not intended to be complete, but they emphasize interpretations of fossil characters that differ from previous analyses (e.g., Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992). Sometimes the differences in interpretation are based on new information, either from recent literature or direct reinvestigation (e.g., our reinvestigation of the "cupule" of *Caytonia*). Other differences reflect reinterpretation based on the same data available to other workers; in such cases, we hope that we have simplified interpretations and made them less dependent on a priori phylogenetic hypotheses, but of course such character interpretations of fossils are always open to debate. In cases where we have interpreted certain homologies in fossil taxa differently from authors of previous analyses, we discuss these differences in some detail in both the discussion of characters and the discussion of the fossil taxa. We also have changed some of the terminal units in the analyses in line with recent fossil discoveries so that there is less character polymorphism in the terminals. In these instances we have provided more detailed descriptions of the fossils in conjunction with establishing new terminal units.

FOSSIL PROGYMNOSPERMS

Aneurophyton. *Aneurophyton* is typically included in phylogenetic analyses of the seed plants as an outgroup terminal, and we follow this tradition here. Other Aneurophytales, such as *Tetraxylopteris* and *Rellimia*, are better known but apparently more derived in certain characters, e.g., planation of reproductive structures (Bonamo & Banks, 1967; Bonamo, 1977, 1983), and should be included in future analyses. *Aneurophyton* is characterized by three-dimensional branching systems with helical (or possibly sometimes decussate) arrangement of lateral branching, protostelic stems, considerable development of secondary growth, and terminal, fusiform sporangia (Serlin & Banks 1978). Stems include a multilobed strand of mesarch primary xylem surrounded by pycnoxylic secondary xylem and tracheids with bordered pits. The ultimate appendages are three-dimensional, two- or three-times dichotomizing branchlets that are often considered to be homologous with the leaves of more recent progymnosperms. There is some variability in reproductive structures in Aneurophytales, with some taxa having aggregate fertile lateral branches that demonstrate a tendency toward planation as well as appearing to be somewhat circinate (e.g., *Tetraxylopteris*). In *Aneurophyton germanicum* Krausel & Weyland the fertile ultimate branchlets dichotomize once, and the two branchlets curve inward and bear two rows of fusiform sporangia on the inner surfaces. All Aneurophytales that have sufficient preservation have been found to be homosporous (Taylor & Taylor, 1993).

Archaeopterids. *Archaeopteris* is commonly considered to be a composite genus (reconstructed from more than one fossil) that includes frondlike branching systems and trunks of varying size. It is a historically significant genus because it ultimately was the basis of the concept of "progymnosperms." Beck (1960) was able to associate the

coniferous secondary wood of the trunks (*Callixylon*) with frondlike planate branching systems (*Archaeopteris*) based on similar anatomical details. The stem has a eustele of mesarch vascular bundles with pyncnoxylic secondary wood having distinctive bands of circular bordered pits on the radial walls of the tracheids (e.g., Beck, 1960). Carluccio et al. (1966) demonstrated that the ultimate branching systems of planate, variously dissected webbed leaves, were actually spirally arranged on all orders of branching. This supported the interpretation that *Archaeopteris* had planate lateral branching systems and not fronds as originally thought. Anatomical studies by Beck (1971) and Scheckler (1978) have refined further our understanding of *Archaeopteris* morphology, anatomy, and ontogeny and have demonstrated that branches originated from axial primordia and not from axillary buds.

Various hypotheses link the Archaeopteridales to taxa with large frondlike leaves (the "cycadophytes") based on presumed homology of the lateral planate branching system with fronds, as well as to simple-leaved branch systems in coniferophytes (Meeuse, 1963; Beck, 1971). More recently, Rothwell (1982) has suggested an alternative origin of conifers from *Callistophyton*-like ancestors based on common pollen structure and platyspermic ovules, among other characters.

Reproductive structures of *Archaeopteris* are fusiform sporangia borne adaxially in rows along terminal fertile leaflike appendages that are terminally dichotomous (e.g., Beck, 1971). *Archaeopteris* species are considered to be either homosporous or heterosporous, and it has been suggested that as fossil taxa become better known all species will be discovered to have been heterosporous (Phillips et al., 1972). Megasporangia may be larger (Arnold, 1935), or smaller (Phillips et al., 1972) than the microsporangia. Fertile ultimate branches are borne helically on penultimate branches that are arranged in planate branching systems. Devonian seeds on branching systems have been associated with *Archaeopteris*-like plants (Arnold, 1935).

FOSSIL SEED PLANTS

Lyginopterids. *Lyginopteris* has been treated in most previous cladistic analyses of seed plants as a composite taxon (reconstruction) based on several independently described fossil taxa. These include petrified or compressed eustelar stems (*Lyginopteris*), petrified ovules (*Lagenostoma*) within lobed campanulate cupules (*Calymmatotheca*), compressed fronds (*Sphenopteris hoeninghausii* Sternberg), and several types of microsporangiate organs (*Crossotheca*, *Telangium*, *Telangiopsis*, and *Feraxotheca*) that are pinnate and laminar with abaxial sporangia in *Crossotheca* and *Feraxotheca*, but terminal in *Telangium* and *Telangiopsis* (compression fossils with the characteristics of petrified *Telangium*). Stems, leaves, and cupules have distinctive capitate epidermal glands (used by Oliver & Scott, 1904, to recognize the "seed ferns"). Stems have anastomosing radially elongate bands of fibers in the outer cortex (Oliver & Scott, 1904). There is considerable variability within the family Lyginopteridaceae as it is usually circumscribed (Stidd & Hall, 1970; Taylor & Millay, 1981; Galtier, 1988) and relationships within and outside of the family will be better understood as new fossil evidence becomes available. In our analyses we have used a broad composite profile for the lyginopterids as our terminal, but anticipate that in future analyses this terminal would be divided into subunits based on observed variation within the group.

Some previous analyses have interpreted branching in *Lyginopteris* as axillary as opposed to dichotomous (Galtier & Holmes, 1982). We interpret the branching pattern of the lyginopterids as dichotomous, but with occasional close dichotomies that superficially mimic axillary branching (see Taylor & Millay, 1981). We do not know of any definitive evidence of axillary branching in this group. At any rate, because of the diversity within the group, it is possible that some taxa referred to as lyginopterids had dichotomous branching while others had axillary branching, or a mixture of both forms of branching. Thus, we have scored our lyginopterid terminal as unknown for the presence or absence of axillary buds/branching.

Medullosans. Medullosans are characterized by their large bifurcate fronds, complicated but fundamentally eustelar stem anatomy, large noncupulate ovules, and complex synangia (Stewart & Delevoryas, 1956; Millay & Taylor, 1979; Taylor & Taylor 1993; Stewart & Rothwell, 1993). They are commonly preserved as compressions and petrifactions and their vegetative and reproductive anatomy and morphology have been carefully and extensively studied (e.g., Delevoryas, 1955; Stewart & Delevoryas, 1956; Millay & Taylor, 1979; Taylor, 1965, 1971; Taylor & Eggert, 1969; Eggert & Rothwell, 1979; Mapes & Rothwell, 1980; Stidd, 1981, 1990; Dufek & Stidd, 1981; Rothwell & Eggert, 1986), although complete suites of vegetative and reproductive characters are not known for all of the petrified stem taxa. Interpretations

of the stem anatomy and the origin of the synangiate prepollen organs have been subjects of considerable controversy (Eggert & Rothwell, 1979; Rothwell & Eggert, 1986; Stidd, 1990) and there is variation in key vegetative characters within the genus as it is presently circumscribed. *Medullosa endocentrica* Baxter (Baxter, 1949) appears to have a different growth habit (vine vs. tree) and mode of branching (it is the only medullosan with axillary branching; Hamer & Rothwell, 1988). We have encoded the characters of medullosans with treelike growth habit that do not have axillary branching. In future analyses, pending availability of characters, we will add the axillary branching medullosans as an additional terminal unit. Our coding of characters has not been affected by controversies over the origin of the polystelic stem of medullosans or about the homology of the large and complex pollen-bearing organs.

Callistophyton. The Callistophytaceae were first recognized and circumscribed by Delevoryas & Morgan (1954) when they demonstrated that petrified axes superficially similar to *Cordaites* were actually very similar in morphology to the stems of *Lyginopteris*. The vegetative and reproductive anatomy and morphology have subsequently been carefully described. Stidd & Hall (1970) were able to demonstrate the association between ovules of the genus *Callospermarion* (Eggert & Delevoryas, 1960) and fronds of *Callistophyton*. Subsequent studies by Rothwell (1972a, 1975, 1980, 1981) have made the genus one of the best known of the Paleozoic pteridosperms.

Callistophyton is reconstructed as a shrubby plant with spirally arranged fronds with axillary branches and occasional adventitious roots at the nodes. Synangia and ovules were borne on the abaxial surfaces of pinnules. Ovules were not borne in cupules and were platyspermic with the nucellus free from the inner integumentary layer except at the base. Synangia consisted of a ring of laterally fused elongate sporangia. Pollen-bearing organs include *Callandrium* (Stidd & Hall, 1970) and *Idanothekion* (Millay & Eggert, 1970). Pollen in these organs and pollen found in the micropyles of *Callospermarion*-type ovules is of the *Vesicaspora* type, monosaccate with a distal sulcus and two lateral lobes. The pollen is often well preserved and has been found with an intact branched pollen tube (Rothwell, 1972b) and with apparently intact microgametophytes within the walls (Millay & Eggert, 1970, 1974) that are similar to those in extant conifers. These similarities have led to speculation about the relationship between the Callistophytaceae and cordaites and even conifers (e.g., Rothwell, 1982; Stewart & Rothwell, 1993). This is one of the questions best answered in a phylogenetic context and we address the possibility of a callistophytacean–conifer relationship below.

Cordaites. Cordaites constitutes a conspicuous group of plants in many Late Paleozoic floras of the Northern Hemisphere. The earliest descriptions of cordaites were based on the large strap-shaped or lanceolate leaves of *Cordaites* and associated wood and reproductive organs from Europe (Feistmantel, 1876; Grand-Eury, 1877; Renault, 1879). Subsequently, a number of new cordaitalean taxa have been established from other areas and incorporated in three distinct families: Cordaitanthaceae (Cordaitaceae), Rufloriaceae, and Vojnovskyaceae (Meyen, 1984, 1988). The Cordaitanthaceae include Euramerican taxa, while the two other families are based on Angaran forms. There is considerable structural variation among members of the three families, particularly regarding the reproductive organs. The Euramerican cordaites are better understood than the Angaran forms because of abundant petrified material. Reviews of taxa included in the three families were given by Meyen (1988) and Rothwell (1988). The Cordaitanthaceae include wood (*Cordaixylon*, *Mesoxylon*), pith casts (*Artisia*), roots (*Amyelon*, *Stelastellara*), leaves (*Cordaites*), male and female cones (*Cordaitanthus*), male cones (*Gothania*), seeds (e.g., *Cardiocarpus*, *Mitrospermum*, *Samaropsis*), and pollen (*Felixipollenites*, *Florinites*, *Sullisaccites*). There appear to be at least two groupings of taxa: the *Cordaixylon–Cordaites–Cordaitanthus–Florinites–Cardiocarpus* complex, considered in the present study, and the *Mesoxylon–Cordaites–Gothania–Felixipollenites/Sullisaccites–Mitrospermum* complex, but there are other groupings not yet fully understood (e.g., Rothwell & Warner, 1984; Trivett & Rothwell, 1985, 1988; Rothwell, 1988).

The cordaites were tall, profusely branching trees, or smaller trees or shrubs (Rothwell & Warner, 1984), with eustelic, pycnoxylic wood and spiral phyllotaxis. Stems of *Cordaixylon* are endarch, while those of *Mesoxylon* are mesarch. Secondary xylem pits are araucarioid (e.g., Renault, 1879; Scott, 1912; Rothwell & Warner, 1984; Trivett & Rothwell, 1985). The pith is conspicuous, typically with a septation of parenchyma tissue.

Foliage comprises large strap-shaped, spatulate or narrow grasslike leaves (*Cordaites*), and at least in some species also small scale or needlelike leaves around buds, at the base of branches or extending

along the branches (Rothwell & Warner, 1984; Rothwell, 1988). There is no mid-vein in *Cordaites*, but numerous, densely spaced, dichotomizing veins that run almost parallel in the leaf lamina.

A detailed account of the organization and structure of the microsporangiate and ovulate cones of *Cordaitanthus* was given by Florin (1950, 1951). The pollen-bearing and seed-bearing cones are similar in basic form; they are compound, and consist of lateral branches borne on a central bracteose axis, either in a planate pattern or spirally arranged. Each lateral branch has a number of spirally arranged scalelike sterile appendages interspersed with sporophylls. These are simple, laminar, with an apical cluster of four to six free microsporangia. Dehiscence is by longitudinal slits toward the center of the sporangial cluster. Pollen grains found in situ in *Cordaitanthus* are similar to dispersed grains assigned to *Florinites*. They are eusaccate, monosaccate, and inaperturate (Florin, 1936; Millay & Taylor, 1974). Male gametophytes were observed in the pollen first by Renault (1902) and later described in detail by Florin (1936). Four to five or six nuclei are arranged in a single row oriented towards the distal pole.

The megasporophylls are stalklike, and in the more recent forms are simple, bearing a single, terminal ovule (*C. zeilleri* Renault), or in the older forms dichotomous, bearing two ovules (*C. pseudofluitans* Kidston). Dispersed and petrified seeds associated with *Cordaitanthus* are assigned to *Cardiocarpus*. The ovules are platyspermic with a single integument consisting of an inner sclerotesta and an outer sarcotesta. A single vascular strand enters the ovule and gives rise to one pair of vascular bundles that pass up through the integument and another pair of vascular bundles that pass into the nucellus. The nucellar cuticle is distinct and free from the integument and thick megaspore membrane.

The microsporangiate cone, *Gothania*, associated with *Mesoxylon*-type wood (Hirmer, 1933), is similar to the compound cone of *Cordaitanthus* in general structure, but differs in having sporangia arranged in a single row at the apex of the sporophyll. Pollen grains found in situ in *Gothania* are eusaccate and monosaccate, with a distinct proximal trilete scar, similar to dispersed pollen of the *Felixipollenites* or *Sullisaccites* type (Millay & Taylor, 1974; Trivett & Rothwell, 1985). Ovules of *Mitrospermum* are linked to *Gothania* by the presence of *Felixipollenites* pollen in the micropyles (Taylor & Taylor, 1993). They are similar to *Cardiocarpus* in most features, but the integument vasculature forms a characteristic tracheal plate, and nucellar vasculature is lacking (Taylor & Stewart, 1964).

Glossopterids. The glossopterids, the signal group of the Gondwana flora, are based on an imprecisely understood assemblage of variously preserved fossils including leaves, stems, roots, and a wide range of reproductive structures (e.g., Delevoryas, 1969; Pant, 1977; Schopf, 1976; Gould & Delevoryas, 1977; Retallack & Dilcher, 1981; Pigg, 1990; Taylor & Taylor, 1993). An excellent overview of pre-1985 literature on glossopterids is provided by Crane (1985) and there have been several interesting and significant studies since that time, including analyses of petrified material from Antarctica (Pigg, 1990; Taylor & Taylor, 1993; Pigg & Taylor, 1990, 1993).

The leaves have a multiveined midrib with anastomosing lateral venation that is not hierarchical with respect to vein order diameters (e.g., Pigg, 1990), and our coding of venation reflects this distinction. In this character, the leaves are similar to those of *Sagenopteris* (considered to be the leaf form of *Caytonia*).

There is a great deal of variation in the nature of ovuliferous and pollen-bearing organs. Reproductive structures termed "glossopterid" include seeds or pollen-bearing sporangia on simple or branched stalks subtended by foliar structures, with the stalks variously adnate to the foliar structures; sometimes the seeds are apparently borne directly on the foliar structures. In some petrified ovulate structures, the ovules appear to be completely enclosed by a foliar organ. Within the envelope, the orthotropous ovules are connected by a network of parenchyma cells that might be interpreted as participating in pollination (e.g., Thomas, 1958; Pant & Nautiyal, 1965; Gould & Delevoryas, 1977; Pant, 1977; Taylor & Taylor, 1993). Pollen-bearing organs consist of variously branched axes terminating in clusters of microsporangia that contain bisaccate and apparently quasisaccate pollen (Surange & Chandra, 1975; Gould & Delevoryas, 1977; Meyen, 1987). There has been some uncertainty expressed in the literature about the nature of these reproductive structures (i.e., foliar vs. axillary). Based on the full range of forms, the apparent axillary nature of the seed stalks, and the occurrence of additional opposing bracts in some taxa, we regard these structures as axillary branch systems with variously modified fertile appendages, adnate to a subtending bract. Thus, in encoding the characters for *Glossopteris*, in contrast to pre-

vious analyses (e.g., Crane, 1985), we have interpreted the pollen and ovuliferous structures as axillary and not foliar. The close association of and/or fusion of fertile axillary structures to foliar appendages is consistent with the morphology of reproductive structures in most other seed plants with axillary branching, such as the conifers, *Ginkgo*, and gnetopsids, and is also consistent with some interpretations of the angiosperm carpel/placenta complex. This interpretation of the seeds as borne on axillary structures is suggested by many of the impression specimens of various glossopterids, both ovulate and pollen-bearing. It is also consistent with both our interpretation of, and the recent literature on, other Mesozoic seed fern fertile appendages, such as in corystosperms and peltasperms, as axial systems as opposed to megasporophylls (Taylor & Archangelsky, 1985; *Antevsia*, Friis & Pedersen, in prep.).

Recent discovery and careful analyses of petrified axes of *Glossopteris* provide additional morphological and anatomical characters that have not been available in the past (e.g., alternate (spiral) phyllotaxy; *Araucarioxylon*-like wood; endarch primary xylem; Pigg & Taylor, 1993). Some of these characters (e.g., *Araucarioxylon*-like wood) are shared with certain Mesozoic seed fern taxa (Table 1; Pigg & Taylor, 1993).

The diversity encompassed within the glossopterids, while imperfectly understood at the present time, makes it clear that in future analyses they will have to be divided into more than a single terminal, each based on a specific reconstruction. As discussed below, "summary" taxa are problematic, and such problems are exacerbated with groups such as the glossopterids for which there is minimal if any evidence for monophyly.

Peltasperms. The family Peltaspermaceae was established by Thomas (1933) based on the ovulate fossil *Peltaspermum*, the associated *Lepidopteris* leaves, and the microsporangiate structure *Antevsia* from the Triassic of South Africa, Sweden, and Greenland (Thomas, 1933; Harris, 1937). Subsequently, a variety of dispersed leaves (e.g. *Compsopteris*, *Kirjamkenia*, *Meyenopteris*, *Phylladoderma*, *Tatarina*), pollen-bearing organs (*Permotheca*, *Pterispermostrobus*), pollen (e.g., *Monosulcites/Cycadopites*, *Protohaploxypinus*, *Vesicaspora*, *Vittatina*), ovulate organs (*Autunia*, *Peltaspermopsis*), and seeds (*Salpingocarpus*) have been assigned to the Peltaspermaceae (Gormankov & Meyen, 1986; Meyen, 1987, 1988; Kerp, 1988; Poort & Kerp, 1990). There is considerable variation in structure among the peltasperms, and in the present analysis we consider two groupings of taxa: the Late Permian *Tatarina–Permotheca–Protohaploxypinus/Vittatina–Peltaspermopsis–Salpingocarpus* complex known from the Eurasian Angara flora (e.g., Meyen, 1984; Gormankov & Meyen, 1986; Meyen, 1988) and the Late Triassic *Lepidopteris–Antevsia–Monosulcites/Cycadopites–Peltaspermum* complex known from Greenland, Sweden, and South Africa (Antevs, 1914; Thomas, 1933; Harris, 1937; Pedersen, 1981).

The peltasperms were probably woody plants. A system of short and long shoots with spirally arranged leaves was described for *Tatarina* (Gormankov & Meyen, 1986; Meyen, 1988), but otherwise little is known about habit and growth form and no wood has been identified in association with the *Lepidopteris* plant.

Leaves of *Lepidopteris* have generally been interpreted as bi- or tri-pinnately compound with conspicuous tuberculate bodies and folds along the main rachis (Nathorst, 1886; Antevs, 1914). Schimper (1869), in his original description of the genus, described these folds as scale leaves, while Nathorst (1886) believed that they were merely cuticular expansion over the tubercular bodies that had folded as a result of fossilization. A reexamination of well-preserved material from Scania shows morphology and epidermal patterns suggesting that Schimper's original interpretation is correct (Friis & Pedersen, in prep.) and that the "frond" of *Lepidopteris* should be interpreted as a branch system with the main axis bearing scale leaves alternating with lateral branches borne in a planate arrangement. The lateral branches bear scale leaves as well as larger laminar leaves. The laminar leaves are simple or once-pinnate. According to this interpretation the *Lepidopteris* branch system is comparable to that of an *Archaeopteris* "frond" and branch systems of some conifers. Leaves of *Tatarina* are simple, lobed, or once-pinnate. Gormankov & Meyen (1986) also included fossil leaves with palmately dissected lamina (e.g., *Kirjamkenia*) in the Peltaspermaceae, and dichotomous bipinnate fronds have been observed in several Permian leaves (e.g., *Peltaspermum* (*Callipteris*) *martinsii*, Poort & Kerp, 1990). The cuticle is typically very thick in the peltasperms, and epidermal features may be difficult to study in detail. The venation pattern is open dichotomizing, fan-shaped or pinnate, pinnules typically lacking or having an indistinct mid-vein; the stomata are haplochelic and scattered on both the abaxial and adaxial surface (Antevs, 1914; Gormankov & Meyen, 1986; Poort & Kerp, 1990).

The microsporangiate organs of *Antevsia* associated with the *Lepidopteris* leaves have been interpreted as compound, bipinnate microsporophylls in previous phylogenetic analyses (Crane, 1985; Doyle & Donoghue, 1986a, b, 1987). However, reexamination of specimens from Greenland and Sweden (Friis & Pedersen, in prep.) shows that they are branched structures consisting of a prominent mid-axis with spirally arranged lateral appendages that bifurcate once or twice. The ultimate units are laminar, bearing eight elongate and free sporangia in two rows. Dehiscence is by a longitudinal split opening toward the center of the microsporangiate clusters. Pollen grains found in situ in the microsporangia of *Antevsia* are similar to dispersed grains assigned to *Monosulcites minimus* Cookson or *Cycadopites*. They are monocolpate with a smooth outer surface, thick lamellate endexine, and a thick homogenous ektexine (Pedersen, 1981). The microsporangiate organs of the *Tatarina*-complex are only fragmentarily preserved, and their structure is not fully understood (Zalessky, 1929; Gormankov & Meyen, 1986; Meyen, 1988). The material consists mainly of dispersed clusters of microsporangia, while only a small fragment of an axis was described. The dispersed clusters of microsporangia are similar to those of *Antevsia*, although the laminar unit bearing the sporangia is not very distinct from the illustrations. Each cluster consists of up to possibly eight narrow, free sporangia that are fused only at the base either to each other or possibly to a laminar structure as seen in *Antevsia*. Several different species of *Permotheca* were described based on dispersed microsporangia clusters (Gormankov & Meyen, 1986). Species associated with *Tatarina* leaves contain striate quasisaccate (*Protohaploxypinus*) as well as striate asaccate (*Vittatina*) type pollen (Gormankov & Meyen, 1986; Meyen, 1987). *Protohaploxypinus* type pollen was also discovered in situ in the seeds of *Salpingocarpus bicornutus* Gormankov & Meyen and *Vittatina* type pollen in the seeds of *Salpingocarpus variabilis* Gormankov & Meyen (Gormankov & Meyen, 1986). A *Permotheca* species producing *Vesicaspora* is associated with *Phylladoderma* (Gormankov & Meyen, 1986; Meyen, 1988).

The ovulate organs (*Peltaspermum* and *Peltaspermopsis*) consist of a main axis bearing stalked peltate and radially symmetrical discs in a spiral arrangement. The ovulate organs assigned to these two genera are distinguished mainly on the basis of the associated leaves, and Poort & Kerp (1990) indicated that when treated as a form genus, *Peltaspermopsis* should be included in *Peltaspermum* (see also Durante, 1992). In the Triassic *Peltaspermum*-type organs the discs are widely spaced, while in some of the Permian forms (e.g., *Peltaspermopsis*), they form dense heads. Ovules were borne along the lobed margin of the discs. Those associated with *Lepidopteris* are apparently unitegmic with a bent, simple micropylar tube and a free nucellus (Harris, 1932a), but their organization is not fully understood. There are no details on the seeds attached to Permian forms associated with *Tatarina*, but the dispersed seeds of *Salpingocarpus* are believed to be produced by *Peltaspermopsis* (Gormankov & Meyen, 1986). *Salpingocarpus* is described as being platyspermic and unitegmic with the nucellus free from the integument and with a distinct salpinx. The nucellar membrane is thin and closely adheres to the thick megaspore membrane. In *S. bicornutus* the integument at the micropylar area is bifid, while in other species of *Salpingocarpus* the micropylar area is simple (Gormankov & Meyen, 1986).

Corystosperms. The Corystospermaceae are a predominantly Gondwanan group of plants first described by Thomas (1933) based on the ovulate structures of *Umkomasia* and *Pilophorosperma*, the associated dispersed seeds of *Spermatocodon*, microsporangiate structures of *Pteruchus*, and leaves of *Dicroidium* from the Middle Triassic of South Africa.

The discovery of *Dicroidium* leaves attached to *Dadoxylon*-type stems from the Middle Triassic of Antarctica documents a woody habit for at least some corystosperms (Meyer-Berthaud et al., 1992). Previous studies have indicated a possible relationship between *Dicroidium* and *Rhexoxylon* type wood in other parts of Gondwana (South America and South Africa) based on common association and presence of secretory cavities (Archangelsky & Brett, 1961; Archangelsky, 1968). It is possible that several wood types were present in the corystosperms. The leaves (*Dicroidium*) are once-pinnate with dichotomizing mid-vein (e.g., Thomas, 1933; Townrow, 1962; Anderson & Anderson, 1983).

The microsporangiate structures of *Pteruchus* consist of a central axis with stalked lateral appendages, each unbranched and terminating in a laminar-peltate structure bearing 20–100 abaxially arranged sporangia. The sporangia are free and dehisced by a longitudinal slit (Thomas, 1933; Townrow, 1962). A spiral arrangement of the lateral units was illustrated for several specimens of *Pteruchus* by Thomas (1933) and further de-

scribed for material from India (Pant & Basu, 1979), which indicates a branching system rather than a foliar nature for *Pteruchus*. Pollen grains are quasisaccate or eusaccate (Taylor et al., 1984; Yao et al., 1992; Zavada & Crepet, 1985).

The ovulate structures of *Umkomasia* and *Pilophorosperma* are compound branching systems consisting of a central axis with lateral branches arising in the axils of bracts. The branches are apparently arranged in one plane (e.g., *U. polycarpa* Holmes) or are spiral (e.g., *U. sessilis* Holmes) (Holmes, 1987). One to several pairs of stalked or more rarely sessile ovulate units are borne along the lateral branches, the distal pair being distinctly bifurcate, while bifurcation may also account for the paired position of the more proximal ovulate units, but this is less clear. Thomas (1933) described bracteoles subtending the ovulate units in some of the South African specimens, but such bracteoles were not observed in the Australian material described by Holmes (1987). Each ovulate unit consists of an outer recurved and cup-shaped envelopment enclosing a single ovule. The ovule is small with a slightly bent and bifid micropylar tip. It has been described as platyspermic, but no permineralized specimen has been described so far.

Thomas (1933) originally described the fertile structures of *Umkomasia* as branching systems. His interpretation was based on ovulate material in which the lateral appendages were subtended by distinct bractlike structures. The axillary nature of the lateral appendages in *Umkomasia* was later documented by Holmes (1987) from the study of well-preserved specimens from Australia. Bracts were not observed in the microsporangiate structures, and Townrow (1962) interpreted this as an indication of a foliar nature for both the ovulate and the pollen-bearing structure. This view was followed by Crane (1985) and Doyle & Donoghue (1986a, b, 1987), who characterized the fertile structures as being compound pinnate sporophylls. However, the recent discovery of permineralized fragments of *Pteruchus* showing radially symmetrical vascular bundles of the central axis indicates a branch system with spirally arranged lateral units for the pollen-bearing organs (Yao et al., 1992). In our analyses we therefore interpreted the reproductive structures of both sexes as branching systems, not sporophylls.

Caytoniales. Caytonia was originally described as an angiosperm by Thomas (1925). The association of characters that he interpreted as angiospermous included, most notably, a fleshy saclike structure with a stigmalike lip, which enclosed several seeds, possibly in two rows. Pollen grains were found on the "lip," and strands of cuticle extending from the lip to the seeds were taken as remnants of pollen tubes (Thomas, 1925). Later authors have referred to the saclike seed-enclosing structure of *Caytonia* as a "cupule," but care should be taken in using this term until the homology of the structure is more clearly established. The "cupules" of *Caytonia* are arranged along an axis (as interpreted by Thomas) or the rachis of a leaf (as interpreted by some other authors, discussed in detail below).

Caytonia has become an informal name for a composite taxon based on an association of organ genera that includes leaves (*Sagenopteris*), synangiate pollen-bearing organs (*Caytonanthus*), and seed-bearing structures (*Caytonia*; Figs. 1, 2). Similarities in cuticular structure among *Sagenopteris* petioles and both *Caytonia* and *Caytonanthus* axes were noted by Thomas (1925, 1933). Pollen in synangia matches pollen in seed micropyles (e.g., Harris, 1964), and these organ genera are consistently associated at various localities (e.g., Thomas, 1925, 1933; Harris, 1932b, 1940, 1941; Lundblad, 1948; Reymanówna, 1973). Thus, there is considerable evidence that these organs represent the same taxon.

The pollen-bearing organs of *Caytonanthus* are synangiate with 3–5 sporangia and, according to Thomas, are borne on the apparently abaxial surface of pinnate microsporophylls (Thomas, 1925; see also Harris, 1941). Leaves are palmately compound with apparent net venation (Thomas, 1925). Some years later, Harris (1933) published an analysis of new specimens of *Caytonia*, in which he demonstrated pollen in the micropyles of seeds and on that basis refuted the angiospermous nature of Caytoniales. Thomas (1925), Harris, and recently Reymanówna (1973), have made detailed studies of *Caytonia* and more recently, pollen has been studied (Pedersen & Friis, 1986; Zavada & Crepet, 1986).

Although Thomas's original interpretation of *Caytonia* as an angiospermous plant has been rejected by most subsequent authors, efforts have persisted to associate *Caytonia* and the angiosperms based on other interpretations of homology. Such conclusions are based chiefly on an evolutionary model proposed by Gaussen (1946), who interpreted the second integument of angiosperm seeds as homologous with the "cupule" of *Caytonia*. Under the Gaussen model, evolutionary reduction from several seeds to one seed within the incurved "cupule" of *Caytonia* would give rise to an anatropous, bitegmic ovule, as is found in many angiosperms. The "cupule" of *Caytonia* would then

be homologous with the "second" or outer integument of some angiosperms, cycadeoids, and under some interpretations, *Pentoxylon*. The Gaussen model has been directly encoded in the data matrices of some recent cladistic analyses of seed plants (e.g., Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992); along with such encodings, the angiosperms have been treated as a single terminal scored as having anatropous, bitegmic ovules. Encoding such phylogenetic hypotheses, both in terms of the model of transformation and the presumed ancestral state of angiosperms, biases cladistic analyses in such a manner that the results may falsely confirm the original model.

We have reinvestigated material of *Caytonia*, *Caytonanthus*, and *Sagenopteris* in order to better understand the nature of these organs and in particular the caytonian "cupule." Our reinvestigation is based on direct observation of numerous specimens (on loan to W. Crepet from the University of Connecticut Paleobotanical Collection) of all three genera collected at Cayton Bay by Henry N. Andrews and Maurice Wonnacott and prepared by Henry N. Andrews. We have verified features of leaf venation for *Sagenopteris*, sporangial characters for *Caytonanthus*, and we present here the results of scanning electron microscope (SEM) examination of various new preparations of *Caytonia* (Figs. 1, 2). Indeed, our direct reexamination has revealed certain characteristics that have not been published previously and raises questions about some of the features reported by other workers working only with light microscopy (LM).

The *Caytonia* "cupule" or seed envelope is fleshy, saclike, and preserved in various orientations (Fig. 1A, B), often with an attached stalk or "pedicel" (Fig. 1B). The envelope has a proximal stoma with a lip adjacent to the "pedicel" or stalk (Fig. 1B) and encloses 8–10 flattened seeds (Fig. 1C, D), arranged with the micropylar ends oriented toward the center and lip (Fig. 1A). Whether the seeds are attached in more than one row is still uncertain, as is the nature of the vasculature that feeds the seeds, even after examination with both LM and SEM. The inside of the envelope is largely composed of spongy parenchymatous cells, and internally there is no detectable smooth epidermis.

The recurved lip of the envelope (Fig. 2A) is apparently laterally continuous with the pedicel; there is no indication of an envelope wall between the pedicel and stoma, and therefore it appears that the adaxial surface of the pedicel forms the wall of the stoma opposite the lip. This interpretation is reinforced by the papillose nature of the epidermis of the recurved "lip" of the cupule, which intergrades proximally and laterally with the epidermis of the adaxial pedicel (Fig. 2A, B, C). In well-preserved specimens the recurved "lip" can be observed to have channels in the papillose epidermal cells that may have provided access into the interior of the otherwise sealed envelope (Fig. 2A, B). In some cases these channels apparently occur also in the epidermis of the proximal "lip" formed by the adaxial pedicel (Fig. 2B). Our studies of *Caytonia* cupules failed to confirm the tubes/strands first observed by Thomas (1925) and later by Reymanówna (1973) connecting the micropyles of the ovules with the channels in the recurved external lip of the envelope (Fig. 2A, B). We did observe surface channels in the interior walls of the cupules flanked by rows of large parenchymatous cells (Fig. 1B, C) that are possibly continuous with the external channels and might also have appeared to be tubes in the preparations of Reymanówna (1973) and Thomas (1925). It is also possible that their material was better preserved or differently prepared from our material.

Another interesting feature of the Cayton Bay specimens is an apparent residue of preserved solute extending between the lip of the cupule and the proximal pedicel epidermis (Fig. 2C, D). This may be the remnant of solute rich liquid (for which a preservational precedent exists in the pollenkitt observed in Cretaceous in situ angiosperm pollen by Friis et al., 1988) and suggests the possibility of a pollination drop mechanism (as is known for several extant gymnosperms) for moving pollen from the outside of the seed envelope to the micropyles of seeds in *Caytonia*. However, in this case, the pollination droplet would be associated with a group of seeds instead of the micropyle of a single seed.

Because of the orientation of the lip and pedicel, we do not interpret the *Caytonia* "cupule" as an anatropous structure in the sense of anatropous ovules of angiosperms. In angiospermous anatropous ovules, the micropyle is formed by the integuments and is found distal to the point of attachment of the funiculus, except in such cases when the funiculus is adnate laterally to the (outermost) integument. If the ovule is inverted (recurved), the ovule is termed anatropous, and the funiculus is either free or is adnate to the second integument. Thus, in angiosperms with anatropous ovules the micropyle is formed by one or both of the integuments; in contrast, in *Caytonia* the stoma of the seed envelope is formed by the wall of the seed envelope (lip) only on one side, and the pedicel forms the other side of the stoma. In *Caytonia* there is no evidence for either a distal attachment

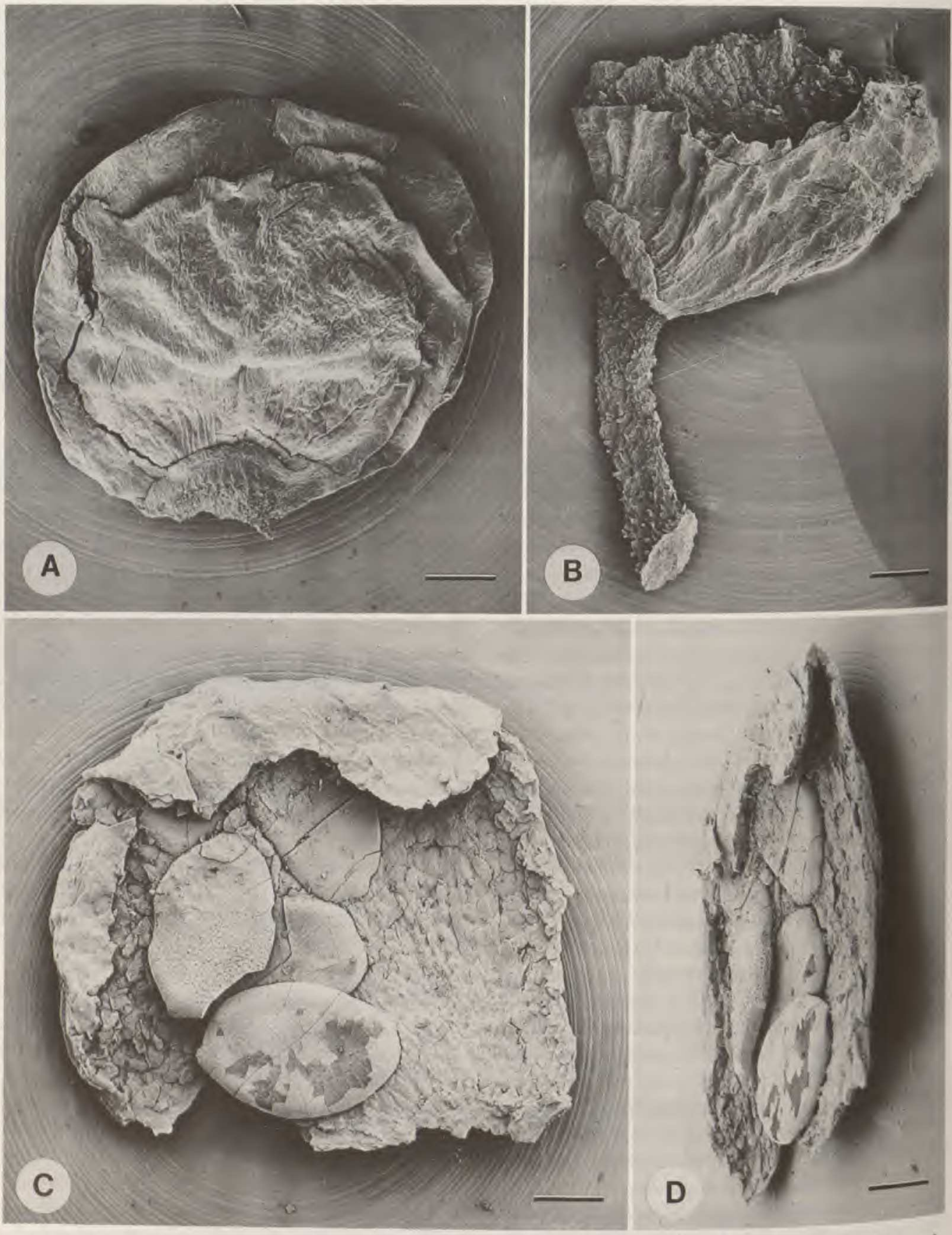

FIGURE 1. SEM preparations of *Caytonia* sp.—A. Fruit compressed dorsiventrally with the pedicel removed, showing the outlines of overlapping seeds. To the right are several folds suggesting a more or less globose form before compression. Scale bar = 0.5 mm, UCPC 6000.—B. A broken fruit with a complete pedicel, showing channels in the large internal epidermal cells and the papillose pedicel epidermis. Scale bar = 0.2 mm, UCPC 6001.—C. A fruit with the abaxial wall removed to show seeds within, apparently borne in two rows and oriented toward the center/lip. Note also the channels in the interior epidermis that are more or less continuous with the openings (toward the bottom of the specimen) from the recurved lip-pedicel interface. Scale bar = 0.5 mm, UCPC 6002.—D. Lateral view of the fruit illustrated in C, illustrating the overlapping seeds. Scale bar = 0.5 mm.

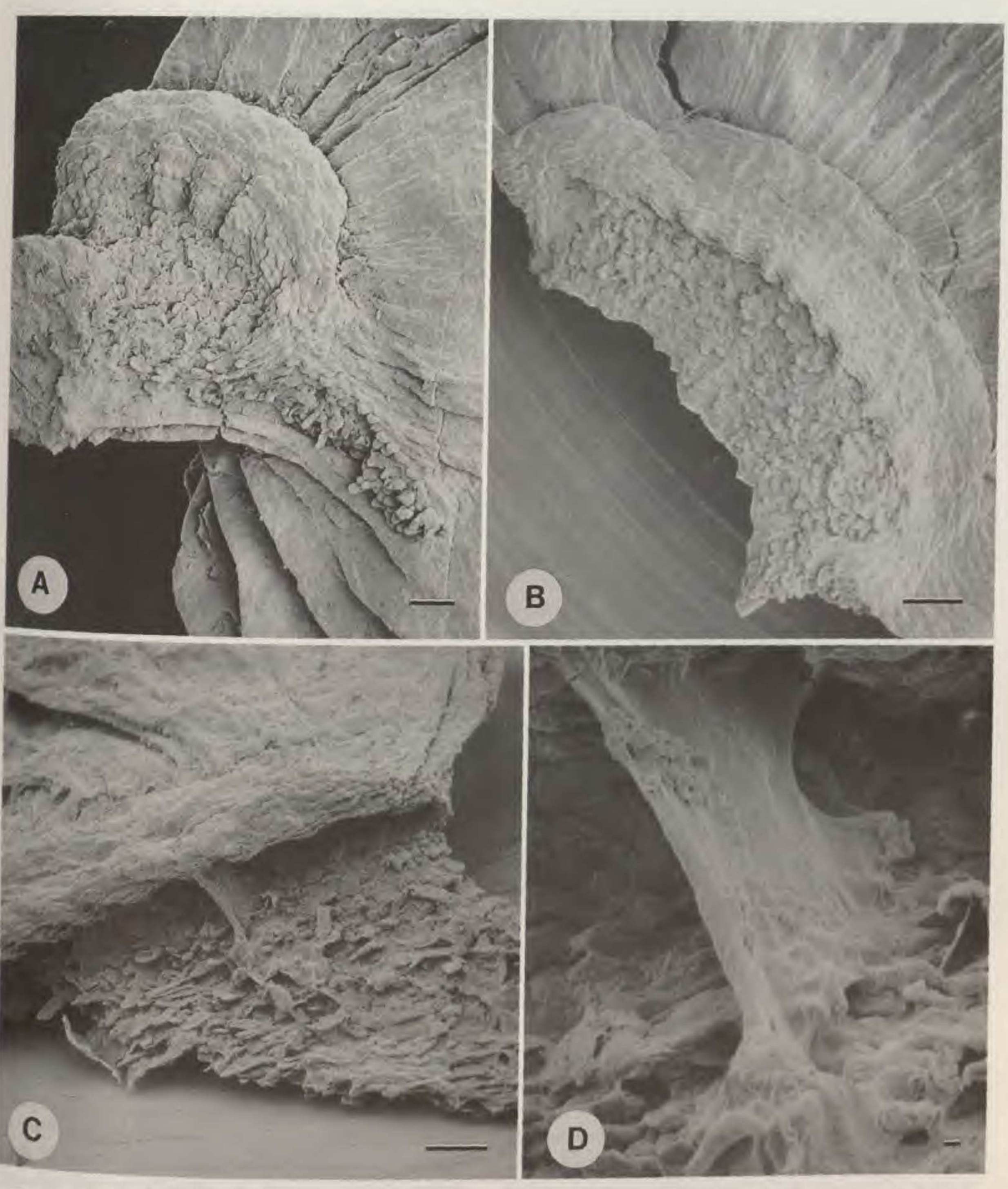

FIGURE 2. SEM preparations of *Caytonia* sp.—A. View of the pedicel-lip interface showing the channels in the recurved lip, the continuity of the lip-pedicel epidermis, and the participation of the adaxial pedicel in the opening into the fruit. Note also the numerous folds in the fossils, again suggestive of its globose nature in life. Scale bar = 0.05 mm, UCPC 6003.—B. The lip of specimen UCPC 6000, illustrating the channels in the lip and the attachment of the recurved lip to the lateral pedicel. Scale bar = 0.1 mm.—C. Lip-pedicel area of UCPC 6001 showing preserved solute that is possibly a remnant of a "pollen drop" or other exudate from lip. Scale bar = 0.05 mm.—D. Higher magnification view of the remains of a pollen drop illustrated in C. Scale bar = 18 μm.

of the stalk or a separate layer that would represent the continuation of the "cupule" (= second integument of authors) between the stalk and stoma. Instead of a structure that is analogous to an anatropous ovule, it appears that the *Caytonia* seed envelope is more similar in form to a planate leaflike appendage that has curved inward upon itself (semicircinate) with connate margins, forming a saclike structure. The seeds that are enclosed might be interpreted as borne directly on the foliar append-

age (envelope), or in our estimation a more consistent interpretation would be that the seeds are borne on an axillary stem system that has become adnate to the subtending bract (envelope). At any rate, given the incurved, not anatropous, nature of the structure, the connation to the stalk, and only partial involvement of the envelope wall in formation of the stoma, it does not appear to be a reasonable precursor of any known ovules with two integuments, much less the specific anatropous bitegmic ovule envisioned by Gaussen (1946). We have encoded the ovules of *Caytonia* as orthotropous and unitegmic, based on observations of their attachment within the "cupule" and the lack of any second layer around each seed. As discussed below, these characters greatly affected the outcome of the analyses of Crane (1985) and Doyle & Donoghue (1986a, b, 1987), and those seeking to evaluate the merits of our results relative to theirs should pay close attention to the treatment of these characters.

Pentoxylon. Pentoxylon is considered to be a small tree with strap-shaped leaves, long and short shoots, leaf cushions on the smaller branches, elliptical ovulate heads, and branching microsporophylls that are arranged in a whorl on a rim that subtends a terminal domelike structure (Bose et al., 1985; Crane, 1985). As used in previous cladistic analyses, *Pentoxylon* is a composite Jurassic–Cretaceous taxon based on both association and structural similarities of petrified and compression-based organ genera (Sahni, 1948; Bose et al., 1985; Crane, 1985). These include stems (*Pentoxylon*, Sahni, 1948), leaves (*Nipaniophyllum* for petrified leaves, Sahni, 1948; *Taeniopteris* for compressed leaves identical to those of *Nipaniophyllum*), ovulate heads of various types such as *Carnoconites* (Srivastava, 1946; Bose et al., 1985), and branched pollen-bearing organs (*Sahnia*) that have been variously interpreted (Vishnu-Mittre, 1953; Bose et al., 1985; Taylor, 1988).

Stems (*Pentoxylon*) are basically eustelic (Beck et al., 1982; Stewart, 1976; Crane, 1985; Taylor & Taylor, 1993), but unusual in a way similar to stems of Medullosaceae (Crane, 1985; Taylor & Taylor, 1993). They have up to 16, but most often five or six, triangular wedges of primary and secondary wood in transverse section. The primary vascular bundles are mesarch and are surrounded completely but unevenly by secondary development of pycnoxylic wood with uniseriate rays that are up to seven cells in height and lack ray tracheids (Crane, 1985; Taylor & Taylor, 1993). There is greater development of secondary wood toward the center of the stem, and this uneven development imparts the triangular cross-sectional appearance to each of the vascular units. There is no axial parenchyma, and radial walls have uni- and biseriate round bordered pits. The bundles are separated by parenchymatous areas analogous to rays, and these are confluent with the pith and cortex, both of which have nests of sclerotic cells, but no resin canals (Taylor & Taylor, 1993). There are some specimens with radially aligned cells in the cortex suggestive of periderm (Taylor & Taylor, 1993). Leaf traces arise in pairs, one from each of a pair of vascular traces (Stewart, 1976).

In petrified *Nipaniophyllum raoi*, strap-shaped leaves up to 20 cm in length have an entire margin and a midrib that extends to the apex and consists of several parallel veins. Lateral veins depart from the midvein at right angles (pinnately) and branch occasionally with the branches fusing near the midvein. The petioles are very short and have 5–9 veins matching the number of bundle scars typically found on the leaf "cushions" of the stems (Taylor & Taylor, 1993). The stomata are confined to the abaxial leaf surface and are sometimes oriented in rows. There have been some questions as to the nature of the subsidiary cells. Sahni (1948) originally reported the stomata as similar to those of bennettitalean leaves (presumably syndetocheilic), but Rao (1976) noted that many were apparently anomocytic (and presumably haplocheilic).

Pollen-bearing organs (*Sahnia*) consist of receptacles about 1 cm in diameter with a raised rim bearing a whorl of delicate axes, approximately 2 cm high. The axes have short, spirally arranged appendages (microsporophylls?) that terminate in clusters of two to four, stalked, thick-walled pollen sacs (Vishnu-Mittre, 1953; Taylor, 1988). Vishnu-Mittre (1953) noted that the microsporangiophores were connate at their bases into a shallow cup and were surrounded by deciduous bracts. Rao (1981) later suggested that these microsporangiate structures were actually free at their bases; Bose et al. (1985) concurred. Vishnu-Mittre (1953) reported scalariform tracheid thickenings in the vascular tissue of microsporangiate structures and short shoots of *Sahnia*, but this was later contested by Bose et al. (1985), who observed no such thickenings.

The pollen is monosulcate, about 25 μm in diameter and has a complex exine structure that appears endoreticulate with an inner lamellate layer (Osborn et al., 1991). Monosulcate pollen has been observed in the micropyles of seeds of *Carnoconites* (see Bose et al., 1985; Crane, 1985, 1988; Taylor & Taylor, 1993).

The seed-bearing organs (*Carnoconites*) asso-

ciated with *Pentoxylon* are unique. They are borne terminally on short shoots and may be ovoid-elliptical or more elongate (Srivastava, 1946). The ovules are orthotropous on short stalks and are not subtended by any discernible structures, nor are there any interseminal scalelike structures as found in the ovulate receptacles of the Bennettitales (Bose et al., 1985). Ovulate heads may be arranged at the ends of laterally branched pedicels or multiple pedicels may emanate from the distal short shoot, each terminating in an ovulate head. The ovules are sessile with a single vascular strand and are crowded together so that they appear polygonal (usually rhomboidal) in surface view (Srivastava, 1946). The seeds are somewhat flattened. The two-layered integument is free from the nucellus except at the chalazal end, with an inner bicarinate sclerotesta and outer fleshy sarcotesta. Details of the cuticles are difficult to determine in the petrified material (Sahni, 1948; Bose et al., 1985), but in macerations of compression fossils of *C. cranwellieae* Harris, Harris (1962) noted that the sarcotesta had a thick outer cuticle, there was a robust nucellar cuticle, and that there was no preserved megaspore membrane. Harris also discovered some isolated delicate cuticles "in the bottom of the maceration pot" that he speculated might represent a thin cuticle of the inner surface of the sarcotesta. Crane (1985, 1986, 1988) interpreted this as evidence for two integuments in the seeds of *Pentoxylon*, but, because of the uncertainty of the true nature of these isolated cuticles and due to the difficulty in observing cuticles in intact material, we chose to score integument number as unknown for *Pentoxylon*.

Because of its unusual nature and the many questions that still surround an interpretation of its morphology, *Pentoxylon* is in need of continued investigation.

Bennettitales (Cycadeoidales). The Bennettitales include two families, Williamsoniaceae and Cycadeoidaceae (Taylor & Taylor, 1993). Bennettitales are well represented in Triassic through Cretaceous sediments and include an interesting mixture of fossils that are very well known (e.g., some species of *Cycadeoidea*) and those that are intriguing, and, possibly phylogenetically significant, but imperfectly understood (e.g., *Wielandiella*, Nathorst, 1909; *Leguminanthus* and *Sturiella*, Krausel, 1948; *Westersheimia*). In some instances it is not entirely clear that these taxa are bennettitalean. Recent direct examination of *Wielandiella* type specimens at the Swedish Museum of Natural History (Friis & Crepet, unpublished) revealed that the reproductive structures are not well enough preserved to unequivocally describe; but cycadeoid affinities, suggested by leaf structure, cannot be ruled out, nor can the bisporangiate condition be absolutely ruled out for these cones. In spite of the uncertainty surrounding several taxa, the Bennettitales have been the objects of considerable attention because of the striking characters they share with flowering plants. They were first described in the nineteenth century (e.g., Buckland, 1827, 1828; Williamson, 1870; MacBride, 1893; Lignier, 1894) and became very well known through the work of Wieland (1906), whose demonstration of cosexual strobili in petrified species of *Cycadeoidea* from the Black Hills of the Unites States was heralded as the discovery of a missing link between the angiosperms and gymnospermous ancestors (Arber & Parkin, 1907). This was, at its time, one of the most widely appreciated contributions of the field of paleobotany to the botanical sciences. The complex bisporangiate structures of Bennettitales are additionally interesting because of the structural variation among taxa and evidence of insect pollination in, at least, *Cycadeoidea* (Crepet, 1972, 1974).

Bennettitales are known from compressions of reproductive structures, leaves, and stems, and as petrifications from a wide range of geographical locations including North America, Europe, India, and Greenland (Delevoryas, 1963, 1968; Crepet, 1974; Harris, 1969; Pedersen et al., 1989; Sahni, 1932).

The Bennettitales vary in habit from delicately branched forms without apparent persistent leaf bases (*Wielandiella*; Nathorst, 1909) to more robust, sparsely branching columnar trunks with persistent leaf bases as in *Williamsonia* (Sahni, 1932) to the familiar ovoid or stout columnar, sparsely branching (*Cycadeoidea* and *Monanthesia* (Wieland, 1906; Delevoryas, 1959). Leaf form varies from entire-leaved taxa to variously regular or irregularly pinnate forms. Cone positions also vary within Bennettitales. They may either be exposed at lateral branch terminals and surrounded only by sterile bracts (*Williamsonia*), or be borne terminally and subtended by two lateral branches (*Wielandiella*), or be terminal on short lateral branches that bear cone-surrounding bracts (*Cycadeoidea*, *Monanthesia*). In the latter instances the short shoots bearing the cones do not extend far enough to elevate the cones beyond the leaf bases that persist on the trunks (*Cycadeoidea*, *Monanthesia*).

As currently interpreted, reproductive structures in the Bennettitales consist of ovulate recep-

tacles that are fleshy and conical or dome-shaped. They bear hundreds to thousands of orthotropous ovules, sometimes with elongated funicles, among sterile interseminal scales with expanded polygonal apices. Tubular micropyles extend beyond the armored surface defined by the tangential walls of the polygonal heads of the interseminal scales.

Microsporophylls in Bennettitales vary in structure around a pinnate groundplan. Microsporophylls are in a single whorl, which in cosexual cones subtends the ovuliferous portion of the receptacle (*Cycadeoidea*, *Williamsoniella*). Sporangia are tubular, and enclosed in elongate or kidney-shaped synangia that are often borne in two rows on the microsporophylls (Wieland, 1906; Delevoryas, 1963; Crepet, 1974).

Many bennettitalean taxa are well known and well preserved (*Cycadeoidea*: Wieland, 1906; Crepet, 1974; *Williamsoniella*: Thomas, 1915; and *Williamsonia* spp.: e.g., Sahni, 1932). However, there are fundamental questions that remain unresolved even in some of the well-known genera. The most basic of these involves the equivocal nature of some of the Upper Triassic Bennettitales (Kräusel, 1948), but there is also some question about the actual distribution of bisexual (cosexual) versus unisexual reproductive structures in Bennettitales. The latter is not as simple a question as it may appear to be. In *Cycadeoidea*, differential maturation times of the pollen and seed-bearing organs led to the assumption that some species were unisexual when they were not, even in well-preserved and carefully examined petrified specimens (Crepet, 1974). Some well-preserved members of Cycadeoidaceae are still relatively poorly understood (e.g., *Monanthesia*) in this regard because they have not been thoroughly investigated. Equivocally identified Bennettitales are, in general, poorly understood, so the association of male and female reproductive structures is far from clear in these taxa. Nonetheless, it does seem unlikely that any of them could have been cosexual. In *Vardekloeftia*, the best known of the Triassic taxa with respect to the ovulate receptacle, the ovulate receptacles were apparently attached by slender stalks and have therefore been presumed to be unisexual (Pedersen et al., 1989). Perhaps the best evidence for unisexual Bennettitales is in the Williamsoniaceae. Several species of *Weltrichia*, a form genus for the compressed microsporangium, appear to have been dispersed without ovulate parts. The variously modified pinnate microsporophylls are fused basally into cups that apparently contain no ovulate receptables (e.g., *Weltrichia spectabilis* Nathorst; *W. whitbiensis* Nathorst; Nathorst, 1911). In some specimens, however (*W. santalensis* Sitholey & Bose, Sitholey & Bose, 1971), the nature of the fossil suggests the possibility that these microsporophylls had dehisced from a relatively broad cylindrical axis as might be expected if they subtended an ovulate receptacle.

Recent analysis of relationships within the Bennettitales have suggested that the group is basally unisexual (Crane, 1988). This finding is congruent with the fossil record of Bennettitales if one excludes *Wielandiella* as too poorly understood to be unequivocally bisexual (and we concur) and if one includes other poorly documented, but apparently unisexual, Triassic taxa in the analysis. Crane's (1988) analysis used *Pentoxylon* as the outgroup and included a complete suite of bennettitalean fossils, but no other seed plants. Many of these taxa, of necessity, had a relatively high number of missing values.

With respect to Bennettitales, our analysis differs from previous broad seed plant analyses in the explicit taxa (reconstructions) we included instead of treating the group as a single terminal, and in our coding of several characters. The use of explicit reconstructions helped us avoid the necessity of scoring the group for presumed ancestral states or as ambiguous states for polymorphisms, as was done by Doyle & Donoghue (1986a, b, 1987). On the other hand, we excluded many bennettitalean taxa for two related reasons: (1) too much uncertainty about their structure or affinities to unequivocally score characters (e.g., equivocally bennettitalean or particularly poorly understood fossils, *Wielandiella*, Nathorst, 1909; *Leguminanthus*, Kräusel & Schaarschmidt, 1966; *Sturiella*, Kräusel, 1948; *Westershiemia*, Kräusel, 1949; *Bennetticarpus*, Harris, 1932b); (2) inclusion of particular poorly known taxa would excessively elevate levels of missing data within terminals. In our initial analyses, we made an effort to include *Vardekloeftia*, but because of limited data we could only score the terminal for approximately 30% of the characters used in our analysis. Thus, *Vardekloeftia* was excluded from our final analyses because it generated massive numbers of cladograms resulting in deresolved consensus trees by uniting with too many disparate groups (for a discussion of this phenomenon, see Nixon & Wheeler, 1991).

We differ from Crane (1988) in our interpretation of the distribution of the corona within the Bennettitales. In contrast to Crane (1988) we code *Cycadeoidea* as having a corona. The anatomical details of the corona, as an apical extension of the ovulate receptacle, are only well understood in *Cycadeoidea*. However, some species of *Cycad-*

eoidea do not have coronas (those with dome-shaped and small ovulate receptacles); our reconstruction and character coding for *Cycadeoidea* is based on *C. dakotensis* Ward. There is a possibility that the corona of *Cycadeoidea* is not homologous with the coronas of the other corona-bearing taxa (e.g., *Williamsoniella*), but this cannot be evaluated until more is known about the structure of the corona in a range of taxa within the order. In *Cycadeoidea*, the corona is not a fleshy extension of the ovulate receptacle, but is made of apparently elongated modified interseminal scales that have elongate cells with spiral thickenings similar to those found in transfusion tissue in conifers (Crepet, 1974). The nature of the tissue composing the corona in *Williamsoniella* is unknown (Thomas, 1915). Another complication is that the "corona" may be more widespread than is known because it will not be detected in petrified material unless the longitudinal section is very close to median (thus, it is difficult to rule a corona out in some species of *Williamsonia*).

It is interesting to note that modified interseminal scales similar to those making up the corona of *Cycadeoidea* are also found at the bases of the ovulate receptacles. It is possible that these areas are modified for conduction of substances that might be associated with pollinator attraction/rewards.

EXTANT TAXA

Cycads. The Cycadales are treated here as three terminals: Cycadaceae, Stangeriaceae, and Zamiaceae. Such a treatment is preferable to a single cycad terminal because it reduces the level of polymorphism and allows more parsimonious constructions of ancestral states within the cycad clade based on observed patterns, not ideal character combinations (Nixon & Davis, 1991). Because of the relatively low diversity of the cycads, and the nature of the characters used in our analyses, we were able to treat the cycad (and conifer) terminals as summary taxa (characters scored for whole monothetic groups) as opposed to exemplar samples, as we were forced to do with angiosperms. The phylogenetic analyses of Stevenson (1990, 1992, 1993) support each of the three cycad families used in our analyses as monophyletic. No fossil cycads were included in our analyses, and the scores assigned to the three cycad terminals are based solely on observation of characters in extant taxa. This treatment differs from that of Doyle & Donoghue (e.g., 1992) who, for example, scored their single cycad terminal as having simple leaves based on the presumed cycadalean affinity of a simple-leaved fossil. The affinity of many presumed fossil cycads with extant families is uncertain or at best equivocal.

Conifers. As with the cycads, the extant conifers were not treated as a single terminal but rather as several terminals along familial delimitations to avoid excessive scoring of polymorphisms. The selected terminals (Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae, and Taxodiaceae–Cupressaceae) are consistent with classical family limits as well as the results of recent cladistic analyses (Hart, 1987; Miller, 1988) at the generic level, although the interfamilial relationships obtained by Hart (1987) and Miller (1988) are quite disparate. The inclusion of Taxodiaceae and Cupressaceae in a single terminal as circumscribed by Eckenwalder (1976) is supported by the results of both Hart and Miller. Our intent is not to produce a complete analysis within conifers, and any conclusions on familial relationships within the conifer clade are tentative.

Gnetopsids. The three extant genera of gnetopsids (*Ephedra*, *Gnetum*, and *Welwitschia*) were treated as separate terminals in all of our analyses. Because our analyses resulted in trees in which these taxa did not form a monophyletic group, we did not analyze any data sets in which the three genera were fused into a single terminal. Particular interpretations of characters for gnetopsids are discussed below and in Appendix A.

Angiosperms. The full data set included 18 angiosperm terminals. These were scored in our matrix for characteristics of the genera represented by these terminals (i.e., states for larger inclusive groups such as families were not extrapolated). The sampling strategy is outlined above. In some analyses, the 18 angiosperm terminals were condensed into a single "angiosperm" terminal, which was scored as polymorphic for all characters that varied among the original 18 terminals.

CHARACTERS

The 103 characters used in our "complete" analysis include vegetative and reproductive morphology, anatomy, and palynology. The discussion below focuses on instances where we have departed from the scoring and/or use of characters in recent studies of seed plant phylogeny, particularly those of Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Several "new" characters have been added in our analyses, and we have scored differently several characters that have been used in previous analyses. In some cases, the differences

from previous treatments involve corrections of errors or the addition of new information, either published or from our reinvestigation of certain fossil taxa.

Unless otherwise noted, all multistate characters have been treated as nonadditive (= unordered). For exceptions, see Appendix A.

Obviously, there is a vast amount of literature available as a source of characters and states for particular taxa. Fortunately, there are also extensive and seminal compendiums of this literature. These works have made the extraction of data much easier and we owe a great deal to our predecessors. Among the more important of these for our study are the works of Bierhorst (1971), Chamberlain (1935), Crane (1985, 1988), Cronquist (1981), Martens (1971), Meyen (1987), Gifford & Foster (1988), Singh (1978), and Taylor & Taylor (1993). Unless otherwise stated, the source of character data can be assumed to be from these works; as much as possible, we have examined the primary references found therein, as will often be apparent by the citations in Appendix A and in the section describing fossils above.

Results of Cladistic Analyses

I. COMPLETE ANALYSIS

Several tree "islands" were found based on randomized spins of taxon order with DADA386 and Hennig86. There were a total of 834 equally parsimonious trees of length 339, retention index (RI) 0.78, and consistency index (CI) 0.38. The strict consensus of these cladograms is presented in Figure 3. A representative tree selected from among the most parsimonious trees is presented in Figures 4–6, with characters mapped. Portions of two other trees are presented in Figures 7 and 8 to illustrate variable positions of *Ginkgo*, *Pentoxylon*, and other seed ferns. If only the extant taxa are considered, the pattern is similar, but not identical, to that found by Loconte & Stevenson (1990), with the cycad clade as a sister group of the remainder of extant seed plants, and the conifer clade as a sister group of gnetopsids + angiosperms, as illustrated in Figures 5 and 8. Important features of the consensus tree include the lack of a monophyletic gnetopsid group and the position of *Ginkgo*, which in some trees (e.g., Figs. 4, 8) is outside of the conifer clade + anthophytes, and in other trees (e.g., Fig. 7) is a member of a broader "conifer" clade. The "higher" or Mesozoic pteridosperms are highly unresolved in the consensus, forming a large polytomy that includes *Ginkgo* as well as the conifer and "anthophyte" clade. Some of the relative placements of taxa contributing to this polytomy are illustrated in Figures 4, 5, 7, and 8, with characters mapped to illustrate character support.

II. FOSSILS EXCLUDED

When fossils were excluded, six most parsimonious trees were found, with CI 0.47 and RI 0.79. No tree islands were noted. The consensus of these trees is presented in Figure 9, rooted to the cycads to facilitate reference to the full analysis. The consensus is highly resolved, with polytomies occurring only within the angiosperm clade. *Chloranthus* is consistently the "first" branch of the angiosperms, with *Ceratophyllum* the next branch. The within-angiosperm topology is consistent with a subset of the trees found in the full analysis. Outside the angiosperm clade, the only differences in topology from that of the full analysis are the position of *Ginkgo*, which when fossils are excluded is outside of the conifer clade in all most parsimonious trees, and the more complete resolution within the extant conifers, with Podocarpaceae as the first branch.

III. SINGLE ANGIOSPERM TERMINAL

When the 18 angiosperm terminals are condensed into a single terminal using the "fuse terminal" option of DADA386, six trees of length 196 (188 excluding autapomorphies), CI 0.50, and RI 0.75 are found. The consensus of these trees is presented in Figure 10. In contrast to the complete analysis, the position of *Ephedra* relative to the other gnetopsids and angiosperms is stabilized, with Bennettitales to the outside. The pteridosperm taxa, which were unstable and joined in a large polytomy in the complete analysis, now show a very stable topology, in which *Pentoxylon* is associated with the "anthophyte" clade as a first branch, and the remainder fall to the outside of the *Ginkgo*–Conifer–anthophyte clade. In these trees, *Caytonia* and the glossopterids always form a monophyletic group.

IV. FOSSILS EXCLUDED, SINGLE ANGIOSPERM TERMINAL

When the fossils were excluded from the data set in analysis III, with a single condensed angiosperm terminal, only one tree of length 110, CI 0.78, and RI 0.85 was found. This tree (Fig. 11) is identical in topology to those found in analysis II (fossils excluded). If only extants are considered, it can be seen that it differs from analysis III (angiosperms condensed) only in having resolved the relative position of Podocarpaceae and Cephalotaxaceae within the conifer clade.

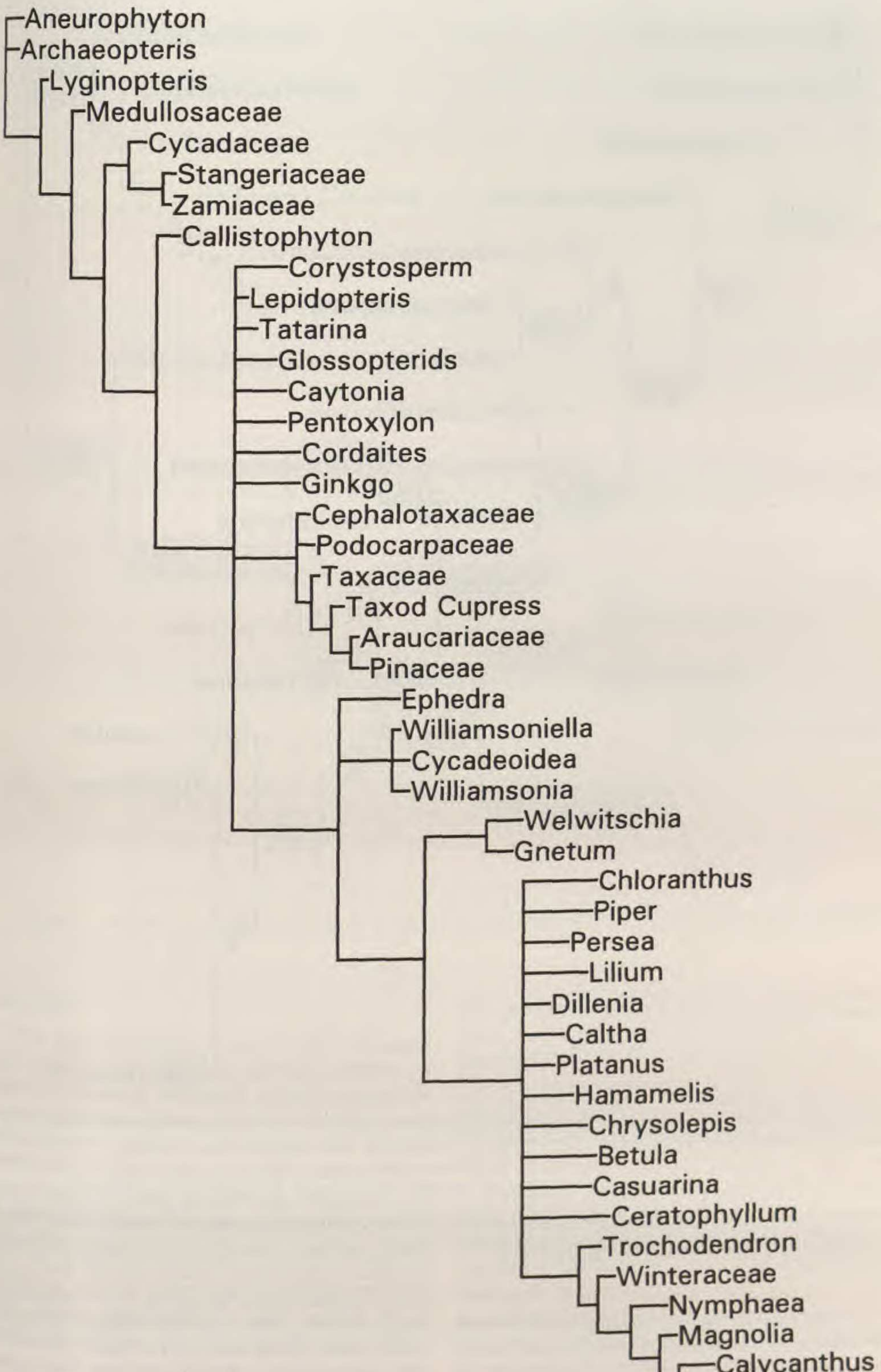

FIGURE 3. Strict consensus of most parsimonious cladograms found for matrix I (full data set).

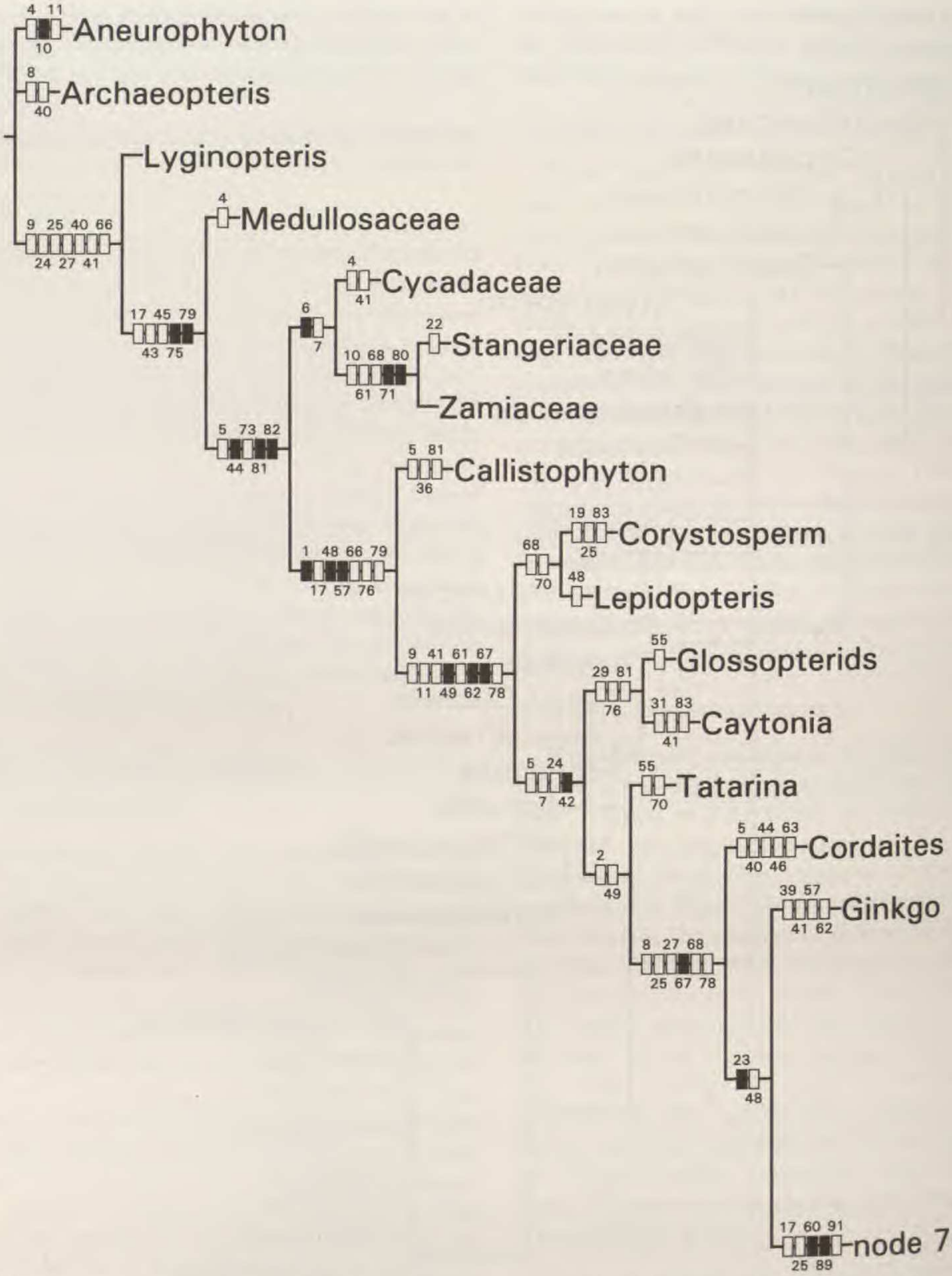

FIGURE 4. Basal section of one of the most parsimonious trees found for matrix I (full data set). Characters are numbered above and below hashmarks. Optimization is arbitrary in some cases where alternative character states may occur at nodes, but length of tree is correct regardless of optimization. Solid black hashmarks represent unique origins of states; open hashmarks represent states not derived uniquely under the optimization presented.

V. FOSSILS EXCLUDED, SINGLE ANGIOSPERM AND CONIFER TERMINALS

Condensing the conifer terminal in addition to the angiosperm terminal, and analyzing the matrix with fossils excluded resulted in only two trees of length 97, CI 0.85, and RI 0.87. The consensus of these two trees is presented in Figure 12. The two trees differ only in whether *Ginkgo* is outside of the conifer clade + anthophytes, or is on the conifer clade. Thus, when only extants are considered, this analysis produced the same two topologies as were found in the complete analysis.

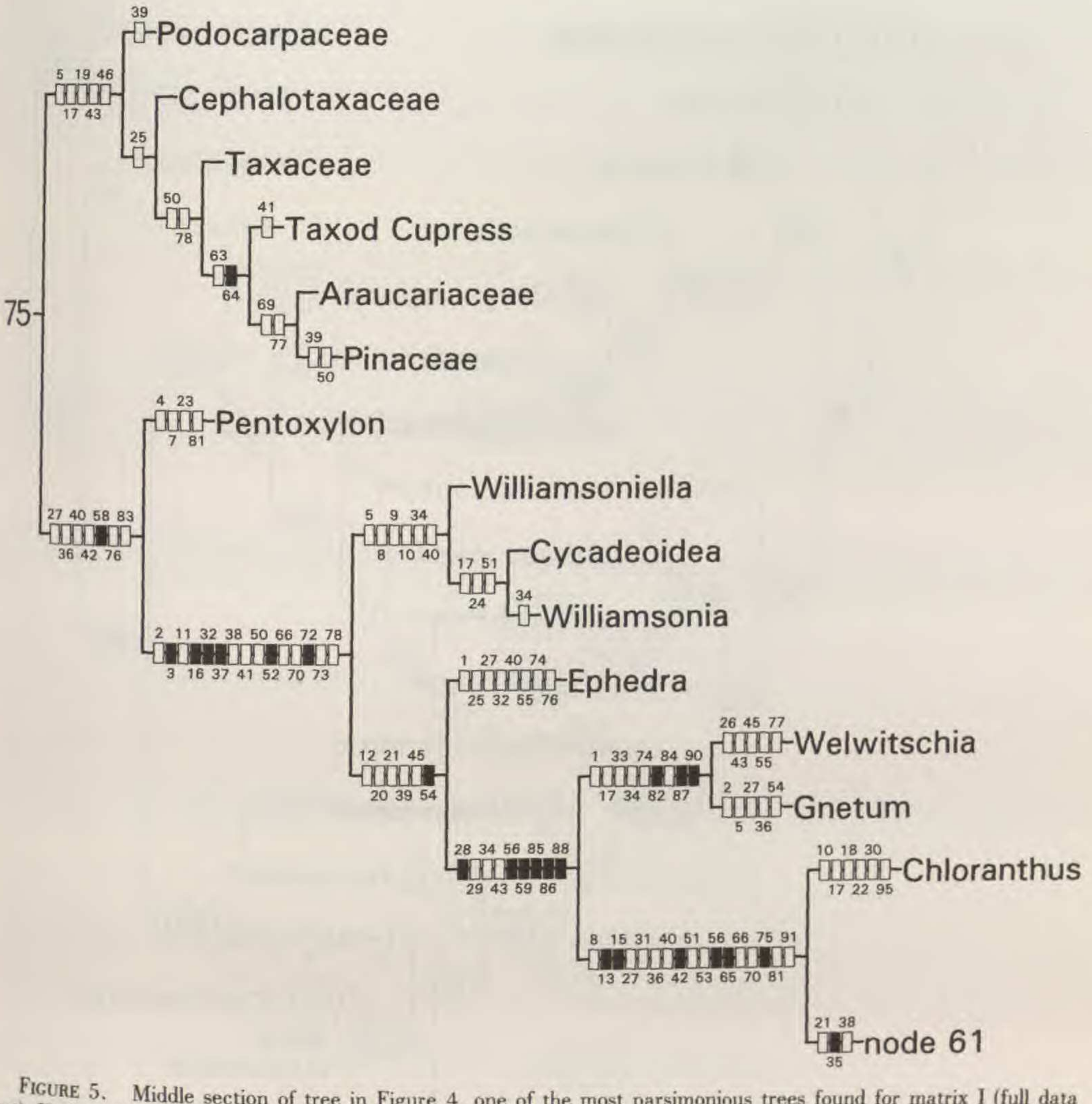

FIGURE 5. Middle section of tree in Figure 4, one of the most parsimonious trees found for *matrix* I (full data set). Hashmarks as in Figure 4.

DISCUSSION

The general pattern of our results for extant taxa conforms most closely with the previous results of Loconte & Stevenson (1990), particularly in the placement of the cycad terminals relative to *Ginkgo*, the conifers, and angiosperms. Considering only extants, in the complete analysis, *Ginkgo* was either a sister group of the conifers, or of a clade that included conifers, gnetopsids, and angiosperms. The latter is the only topology found by Loconte & Stevenson (1990), and by us in the remainder of our manipulations (excluding fossils, collapsing angiosperm and conifer clades to single terminals). Based on our results and those of Loconte and Stevenson, we favor recognition of a "ginkgophyte" group that includes *Ginkgo*, conifers, gnetopsids, and angiosperms. In our opinion, these results help resolve the past difficulty in reconciling certain plesiomorphic features of *Ephedra* that are shared with the conifers, and must be considered homoplasious similarities when cycads are intracalated between the conifers and the gnetopsid–angiosperm clade.

Because of the great similarity of our results to those of Loconte & Stevenson (1990), it would be redundant to go into great detail on characters supporting the "ginkgophyte" clade. Likewise, the characters supporting the "anthophyte" clade (gnetopsids, angiosperms, and Bennettitales) have been discussed in great detail by Crane (1985), Doyle & Donoghue (1986a, b, 1987, 1992), and Donoghue (1989). We therefore concentrate here

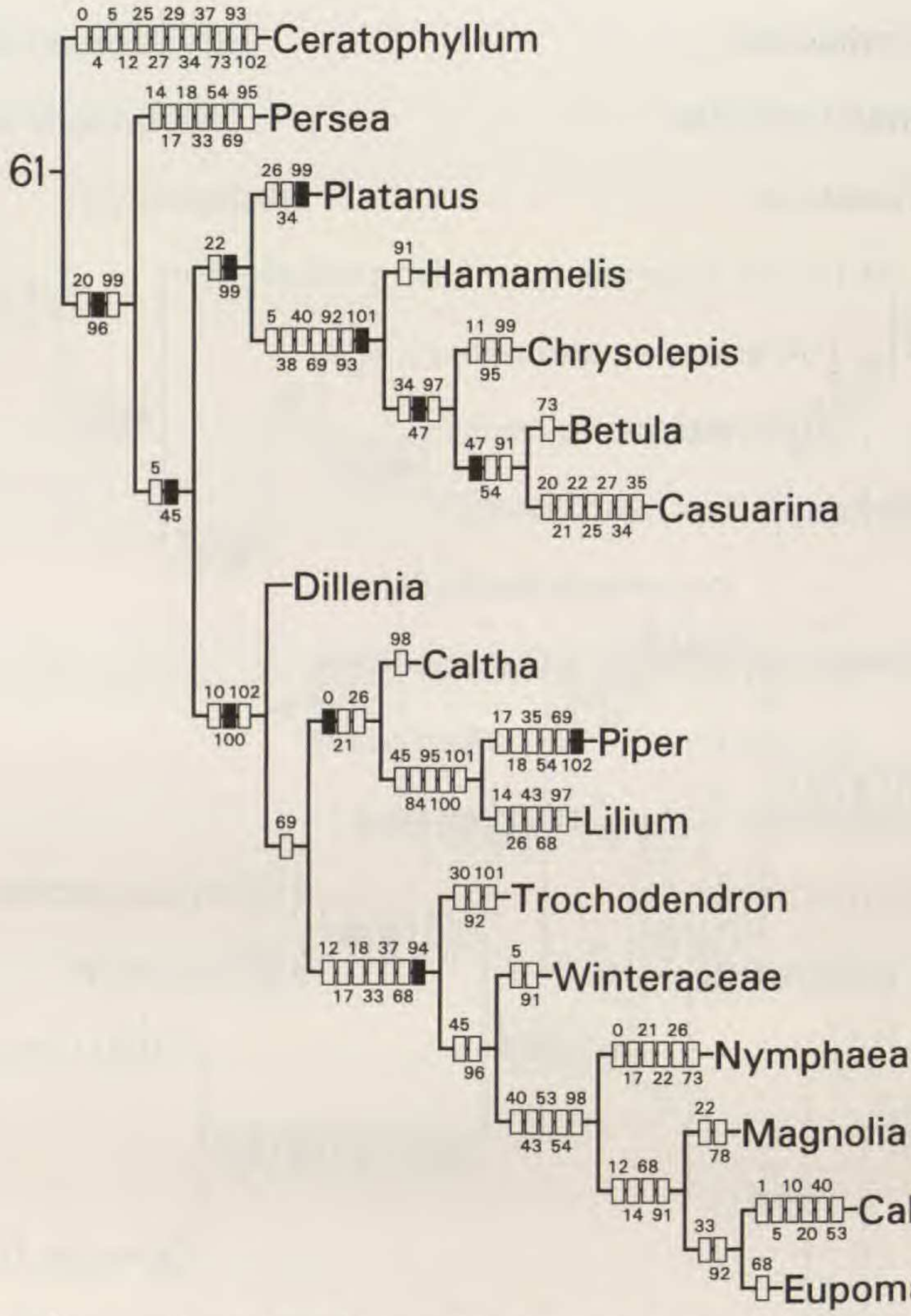

FIGURE 6. Upper section of tree in Figure 4, one of the most parsimonious trees found for matrix I (full data set). Hashmarks as in Figure 4.

on some of the novel clades found in our analyses as well as different character interpretations, which are outlined in Appendix A.

It is clear from comparison of our results with those of Loconte & Stevenson (1990) and Doyle & Donoghue (1986a, b, 1987, 1992) that the inclusion of fossils in the analysis can have a dramatic effect on the major structure of the tree. In particular, based on some manipulations of our data, it appears that certain features of the bennettitalean taxa support association of the "anthophytes" (gnetopsids and angiosperms) more closely with cycadalean features than with *Ginkgo* or the conifers; in our complete analyses, this resulted in *Ginkgo* placed basally on the conifer clade in some of the most parsimonious trees. When fossils are removed, these results are not found, and *Ginkgo* is consistently a sister taxon to the remainder of extant ginkgophytes. Because of the uncertainty in coding numerous characters of the fossil taxa, and, in particular, many of the reproductive and embryological features that most strongly support monophyly of gnetopsids and angiosperms, we view the results of the analyses including fossils as far more tentative than those using extant taxa alone.

In all of our analyses that included fossil taxa, the angiosperms, Bennettitales, and gnetopsids formed a monophyletic group in relation to the remainder of the seed plants. This supports the "anthophyte" clade of previous authors, with the exception that the position of *Pentoxylon* is variable depending on the analysis, and is either placed

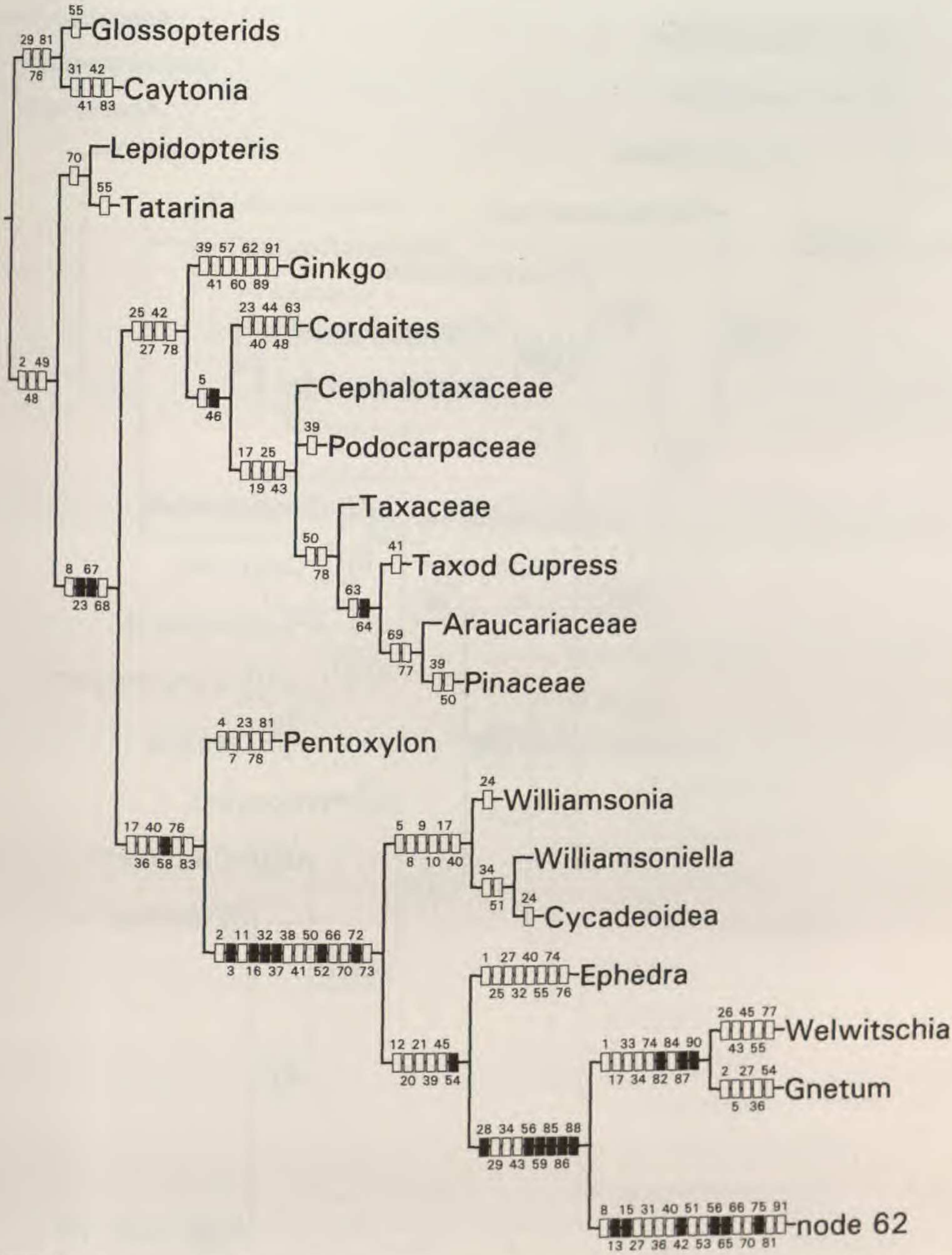

FIGURE 7. Middle section of another most parsimonious tree from analysis I (full data set). Hashmarks as in Figure 4.

as the sister taxon to the core group (Bennettitales–gnetopsids–angiosperms; Fig. 5), or in some cases, may be placed more distantly on the tree, outside of *Ginkgo* (Fig. 8), as reflected in the polytomy in Figure 3. This differs from the placement of *Pentoxylon* as a sister clade of the Bennettitales–gnetopsid group or solely the gnetopsid group in the analyses of Doyle & Donoghue (1986a, b, 1987, 1992) and its closer association with Bennettitales by Crane (1985). This difference is undoubtedly due in part to different codings of various characters, especially a different interpretation of the

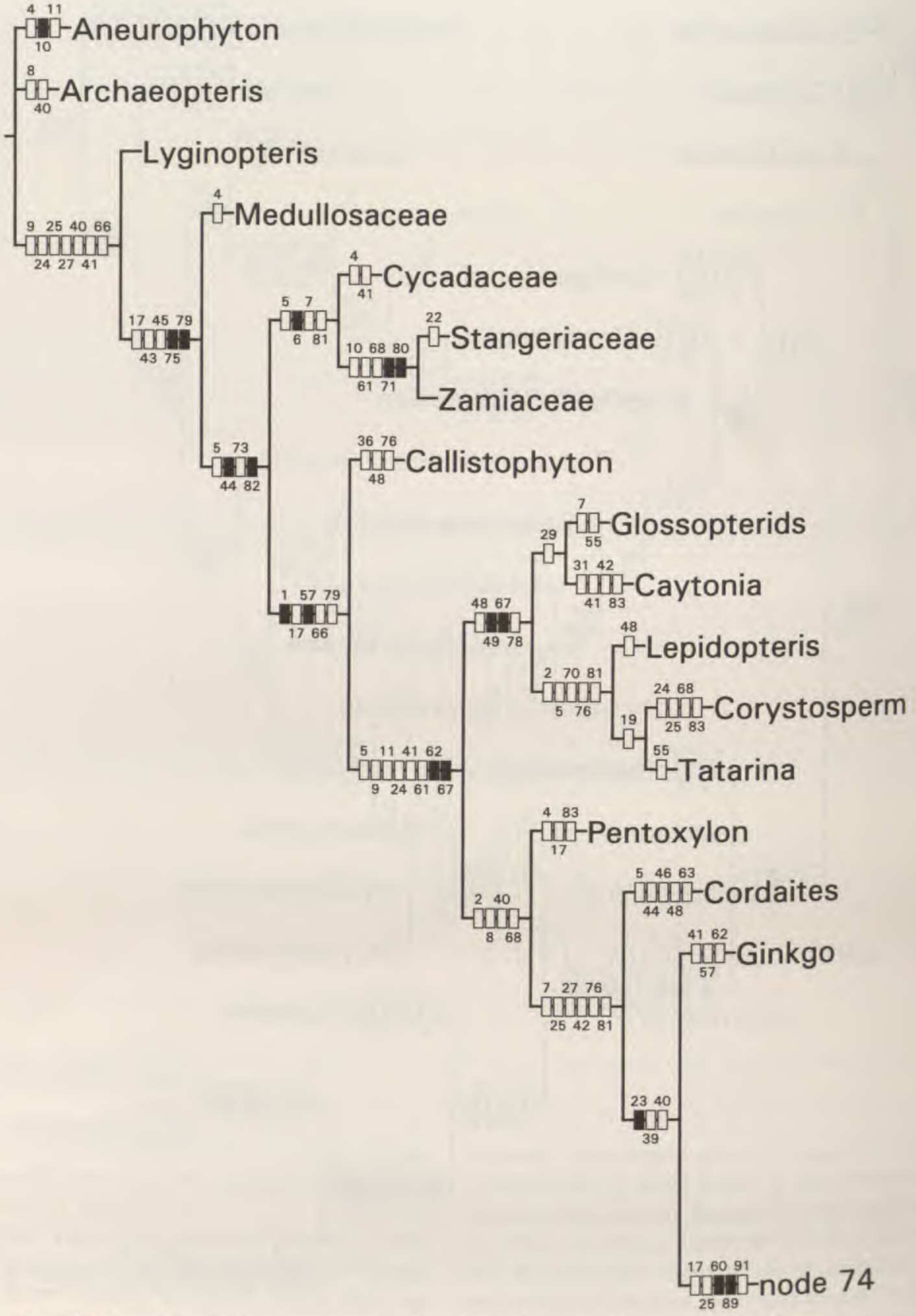

FIGURE 8. Basal portion of a third tree from analysis I (full data set). Hashmarks as in Figure 4.

cupulate structure of *Caytonia* as homologous with a second integument in *Pentoxylon* and the angiosperms. Our conclusion that the "second integument" of *Pentoxylon* has not been conclusively demonstrated resulted in coding of *Pentoxylon* as uncertain for the presence of an outer "seed envelope."

In all of our analyses, the gnetopsids (*Gnetum, Welwitschia, Ephedra*) were paraphyletic in all of the most parsimonious cladograms. However, it should be noted that trees with a monophyletic gnetopsid clade are only two steps longer than our most parsimonious trees in our complete analysis. When fossils were excluded and angiosperms con-

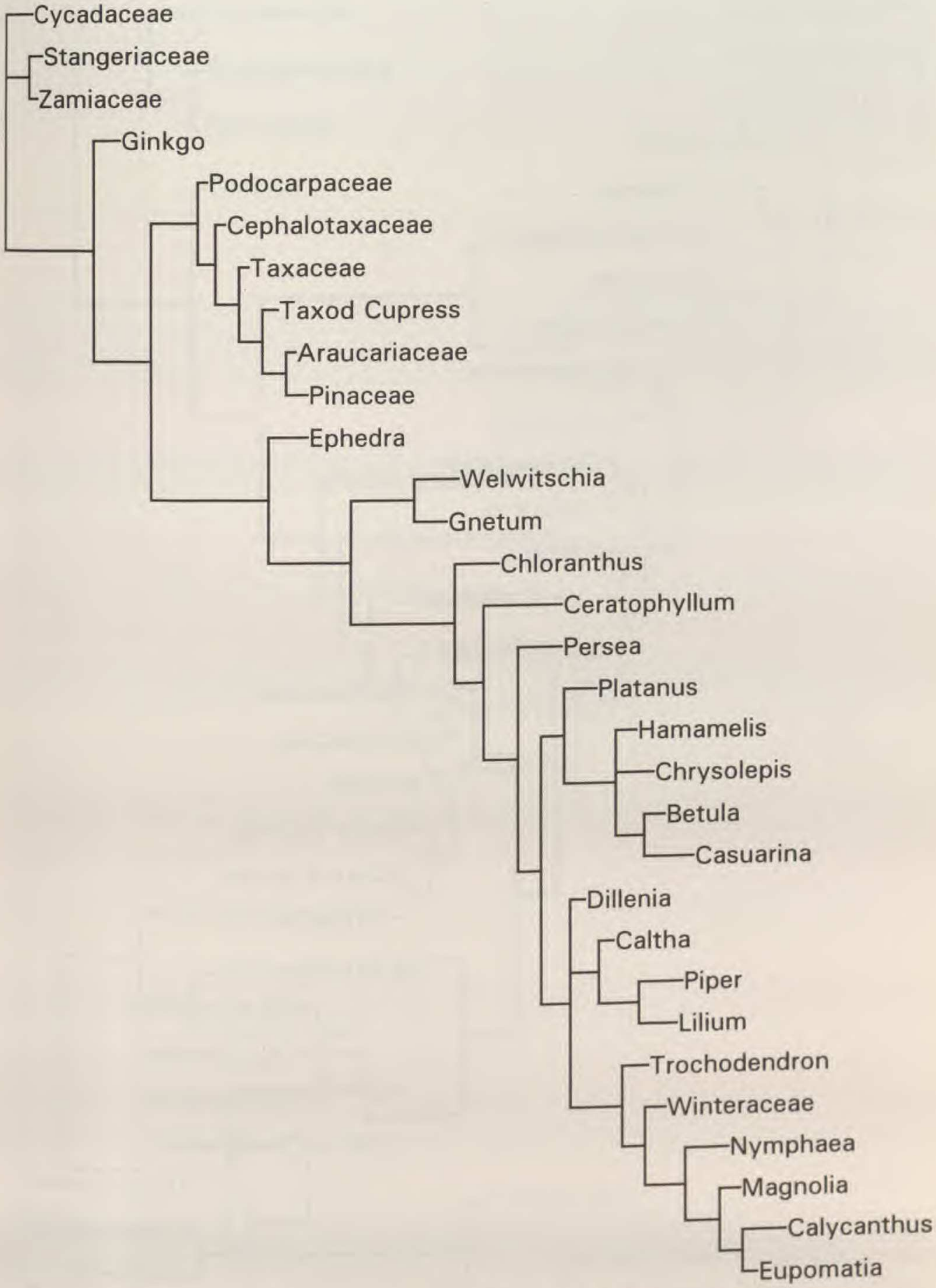

FIGURE 9. Strict consensus of trees found in analysis II (fossils excluded).

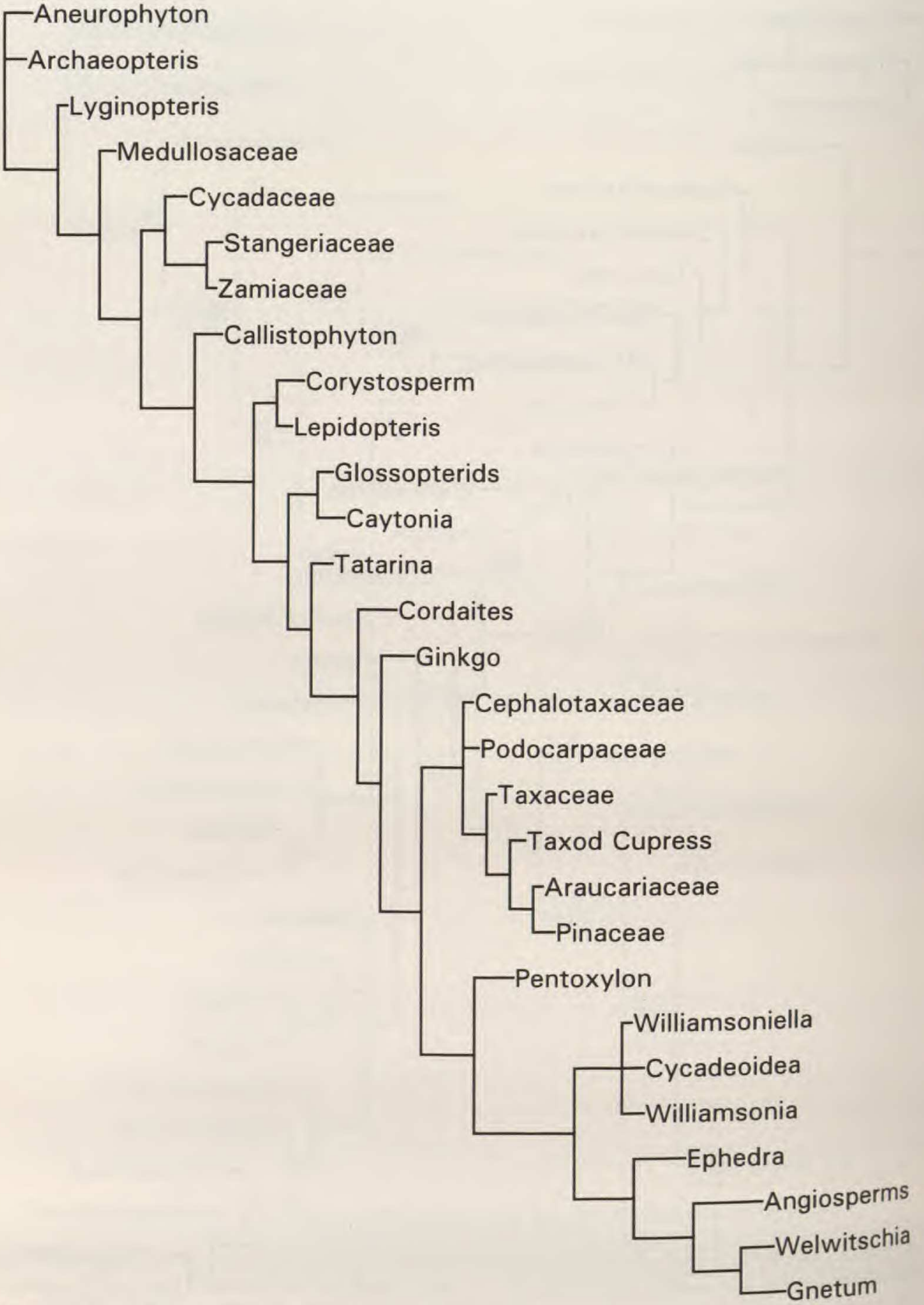

FIGURE 10. Strict consensus of trees found for matrix III (angiosperms condensed to single terminal).

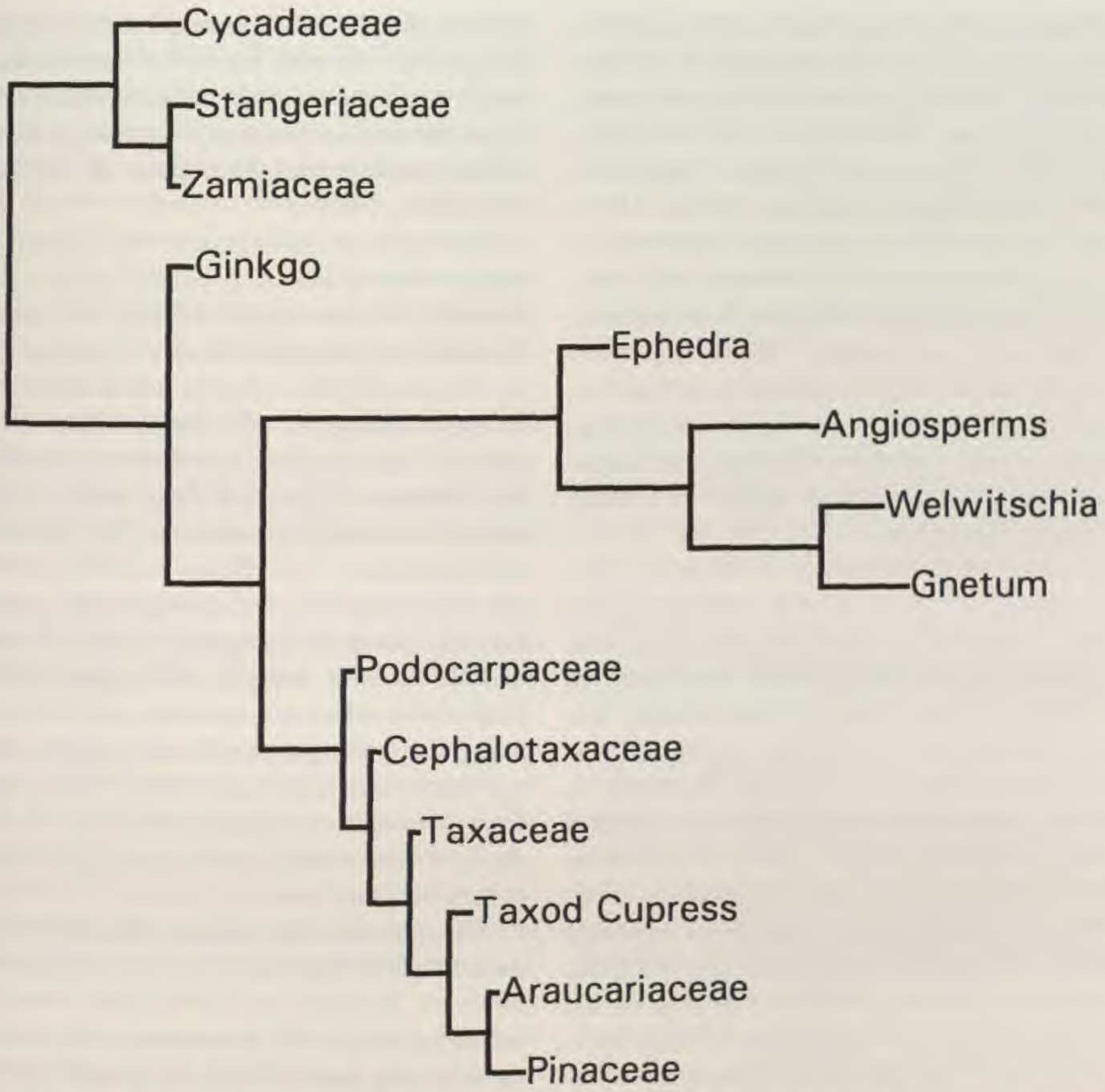

FIGURE 11. Single most parsimonious tree found for matrix IV (fossil tata excluded, angiosperms condensed).

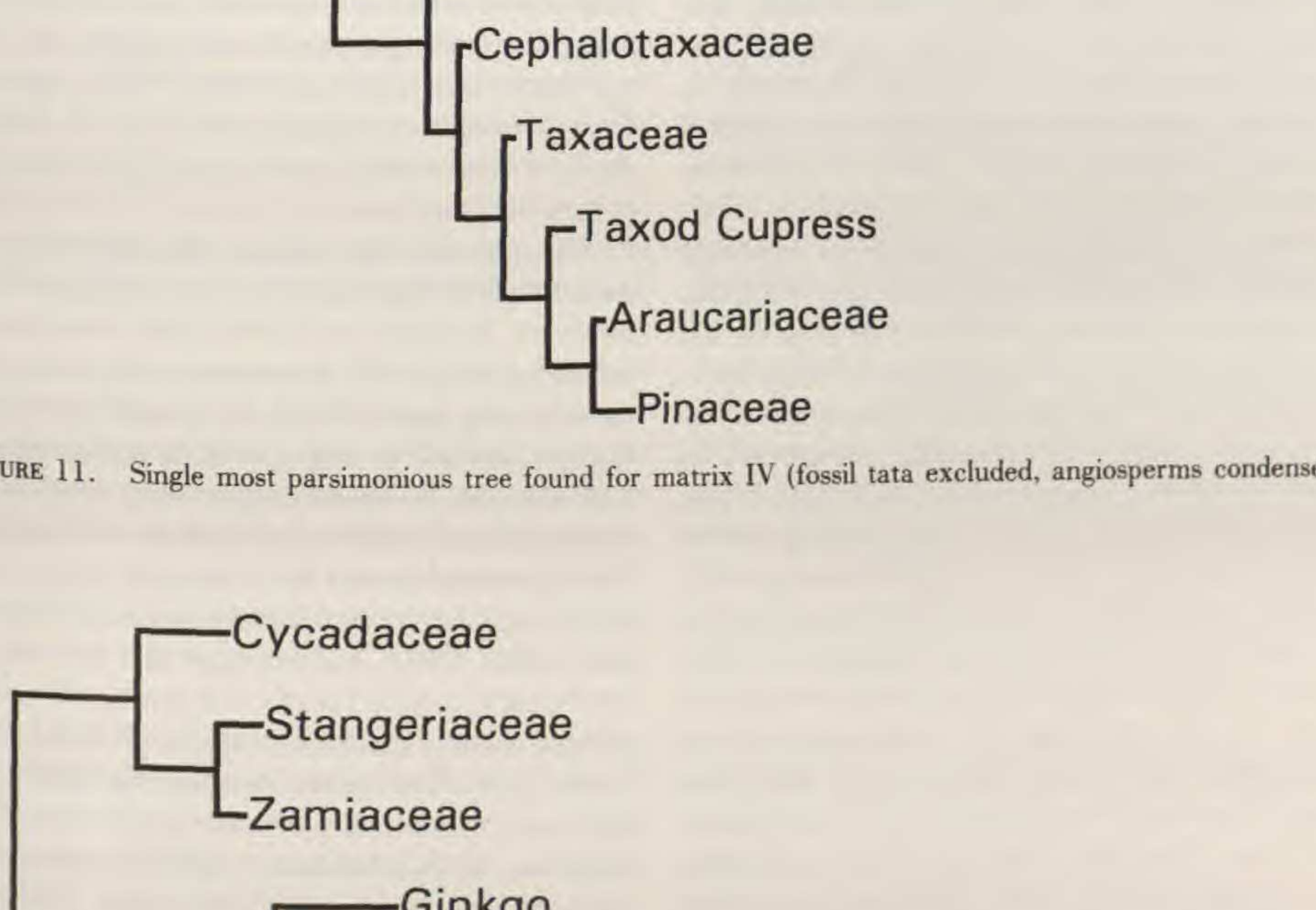

FIGURE 12. Strict consensus of trees found for matrix V (angiosperms and conifers condensed, fossils excluded).

densed (analysis IV), trees with a monophyletic gnetopsid clade were four steps longer (114 steps vs. 110 steps). The characters that support grouping of *Gnetum* and *Welwitschia* with the angiosperms to the exclusion of *Ephedra* include reduction in the microgametophyte, absence of the stalk cell, non-bifid inner integument (bifid only in the earliest developmental stages in *Ephedra*), non-alveolar megagametophyte, absence of archegonia, and cellular early embryogeny. These characters are constant as far as is known in angiosperms; additional characters that vary within angiosperms and support the *Gnetum*–*Welwitschia*–angiosperm grouping include the presence of a tetrasporic megagametophyte.

In all of the complete analyses of Doyle & Donoghue (1986a, b, 1987, 1992), the gnetopsids have been found to be monophyletic, associated with a monophyletic Bennettitales. Donoghue & Doyle (1989), in summarizing previous results, listed "unifying features" of the three gnetopsid genera as: "opposite leaves, circular bordered pits in the vessels, simple microsporophylls, one terminal ovule, and compound strobili." All of these features are either found in one or more angiosperm taxon (sometimes in combination), conifers, or can only realistically be coded as ambiguous in gnetopsids, angiosperms, or both (e.g., whether the angiosperm flower is interpreted as a compound or simple strobilus depends on interpretations of homology of the carpel, and conifers are generally interpreted as having compound megastrobili). We differ from Doyle and Donoghue in our interpretation of the nature of microsporophylls in *Ephedra* and *Welwitschia*, which seem to be clearly compound in both, but simple in *Gnetum* (see Appendix A). The "terminal ovule" of Gnetales, likewise, requires a specific interpretation in order to be scored as *not* homologous with certain angiosperms that have solitary, "terminal" ovules (e.g., Chloranthaceae, Piperaceae, Laurales, Platanaceae, Ceratophyllaceae, to name a few). Such characters are synapomorphies of the gnetopsid clade only when the primitive angiosperm archetype is assumed to lack them, an assumption not supported by observation of a broad array of taxa. Thus, by assuming a particular phylogenetic hypothesis for the angiosperms and extrapolating a primitive type (multiple ovules, foliar carpels = simple strobili, alternate leaves, spirally arranged simple microsporophylls), the character interpretations and coding of Doyle & Donoghue (1986a, b, 1987, 1992) and Donoghue & Doyle (1989) bias strongly against recognizing homologies between gnetopsids and angiosperms, and simultaneously bias their analyses in favor of an isolated, monophyletic Gnetales. This in turn has affected character optimization of the single angiosperm node in their analyses, which was then used as the basis for rooting later analyses within angiosperms (Donoghue & Doyle, 1989; Donoghue, 1989).

Based on our results, and the conflict of these results with those of previous studies (including Loconte & Stevenson, 1990), the question of whether the gnetopsids form a monophyletic group or are paraphyletic relative to the angiosperms (or to the angiosperms plus Bennettitales) remains a question that deserves much more attention. Since the evidence supporting their monophyly in previous morphological analyses was biased by assumptions about the nature of the primitive angiosperm, we feel that the answer to this problem can only be resolved by more careful analyses that include broader samples of angiosperm diversity and additional characters that can be scored unambiguously for gnetopsids and angiosperms. While our study has not resolved this issue, due to the limited sample of angiosperms that we included, the question of gnetopsid monophyly or paraphyly is now reopened.

The question of whether the seed plants are monophyletic was not directly addressed in our analyses, because we only included two terminals (*Aneurophyton*, *Archaeopteris*) that are considered to lack seeds. While the possibility of discovering a diphyletic origin of seed plants existed in our data set, it would require an *Aneurophyton* clade and an *Archaeopteris* clade of seed plants. This question should be addressed with a much larger sampling of both fossil and extant plants that lack seeds. Thus, we feel that the monophyly of seed plants in our results is not a significant conclusion from a cladistic standpoint. However, our "new" character of the bicornute or bifid apex of the seed, which was not used in previous cladistic analyses, is distributed in such a manner that it may provide more information than the "platyspermy-radiospermy" character that is commonly used in argumentation about seed origins. Thus, the cycad–lyginopterid–medullosan nonbifid form of seed might be found to be independently derived from the remainder of seed plants when more data are included. Undoubtedly, other ovule/seed characters can be developed which may help to shed light on this problem.

The proximity of the medullosans and cycads in our results is in contrast to the position of cycads and medullosans in Doyle & Donoghue (1986a, b, 1987, 1992). Our results are consistent with traditional hypotheses of the placement of medullosans

and cycads (e.g., Stewart & Delevoryas, 1956; Stewart & Rothwell, 1993; Taylor & Taylor, 1993) and more similar to the cladistic results of Crane (1985); they suggest that cycads may have originated from an ancestor that resembled medullosans in several respects. We find it difficult to envision the alternative (Doyle & Donoghue, 1986a, b, 1987, 1992; Donoghue, 1989) that the cycads are distant from the medullosans and form a monophyletic group with "anthophytes" excluding the conifers and *Ginkgo*.

Initially, we included four Mesozoic seed fern terminals in our analyses ("peltasperms," "corystosperms," "glossopterids," and "caytonia"), defined in essentially the same manner as Doyle & Donoghue (1986a, b, 1987). In many of those preliminary analyses the four Mesozoic seed fern terminals formed a monophyletic group near the Cordaites–conifer clade (Crepet et al., 1993). In our final analyses, however, we more carefully defined the terminals to be specific reconstructions (*Caytonia*, *Peltaspermum*, *Corystospermum*), as opposed to summaries of groups, and added *Tatarina* (considered to be a "peltasperm"). Of necessity, the glossopterid terminal remained a summary of several glossopterid taxa; we hope that in future analyses this can be remedied. In the analyses reported here, the five Mesozoic seed fern terminals do not consistently form a monophyletic group (e.g., Figs. 3, 4, 7), although they do form a monophyletic group, outside of *Ginkgo*, in some of the most parsimonious trees of our complete analysis. In our complete analysis, the peltasperms and corystosperm terminals move about in the various topologies, sometimes in positions "below" the *Ginkgo* clade and sometimes above the conifer clade, subtending the *Pentoxylon*–"anthophyte" clade. Likewise, *Pentoxylon* is found subtending the anthophyte clade in some trees (e.g., Fig. 5) but is associated with the pteridosperms, outside the *Ginkgo*–conifer–anthophyte clade, in others (Fig. 8).

Glossopterids and *Caytonia* formed a monophyletic group, outside of the ginkgophytes, in some of the most parsimonious trees in our complete analysis (e.g., Figs. 4, 8) and in all of the most parsimonious trees in the analysis that condensed angiosperms to a single terminal (III). This position "below" the *Ginkgo*–conifer–anthophyte clade in all most parsimonious trees in all relevant analyses contrasts sharply with the association of *Caytonia* with the "anthophyte" clade in some previous analyses (Doyle & Donoghue, 1986a, b, 1987, 1992). We interpret these differences to be due to different interpretations of structures (e.g., the "cupule" = second integument interpretation of Doyle & Donoghue, 1986a, b, 1987, 1992), the addition of new data both from the literature and from reinvestigations (e.g., the axial nature of the reproductive structures of *Corystosperms*, glossopterids, and *Caytonia* that were interpreted as sporophylls in previous analyses), and our restriction of some pteridosperm terminals (e.g., *Lepidopteris*) to represent specific reconstructions, as opposed to synthetic "composite" taxa.

In the context of a possible relationship between glossopterids and *Caytonia*, it is interesting to note that *Glossopteris*-like foliage (*Mexiglossa*) is known from the Middle Jurassic of Oaxaca, Mexico, in association with branched axes bearing sporangia that resemble *Caytonanthus* (Delevoryas & Gould, 1971; Delevoryas, 1969; Delevoryas & Person, 1975; Taylor & Taylor, 1993). In combination with our results, this suggests the possibility that the Northern Hemisphere *Caytonia* lineage is derived from an ancestor that is an offshoot of the earlier and highly diverse Gondwana glossopterids (which, of course, may not be monophyletic). Phylogenetic analyses of the Permian–Mesozoic seed ferns, and in particular the glossopterids, in which careful reconstructions of individual taxa are undertaken as opposed to treating them as synthetic groups, is long overdue.

We find the traditional placement of *Cordaites* with the conifer clade in some, but not all, of our fossil analyses. In trees with *Ginkgo* on the conifer clade, *Cordaites* is the "next" branch, as often found in previous analyses (Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992). In contrast, the placement of *Ginkgo* outside the conifer–anthophyte clade is consistent with the notion that it shares numerous plesiomorphic features with Mesozoic seed ferns, but shares few if any synapomorphies that would place it with conifers at the exclusion of the Mesozoic seed ferns. We concur with Qin-er (1993) that the female reproductive structure of *Ginkgo* can be interpreted as an axillary seed-bearing structure subtended by a leaf, these borne on a seasonally determinate structure that may be homologous to the determinate compound cone axis of conifers (but not as densely aggregated nor completely determinate). Thus, the determinate compound strobilus becomes a synapomorphy of the conifer–anthophyte group; and, under such an interpretation, the carpel of angiosperms would be derived from a seed-bearing axis (simple cone = placenta) subtended by a leaf. Such a structure would be homologous to the bract-ovuliferous scale complex of conifers, the leaf-seed-bearing-axis of *Ginkgo*, and possibly to the leaf-

seed-bearing-axis in glossopterids. Such a homology would be general, suggesting that the subtending leaf of glossopterids, and possibly the "cupule" of *Caytonia* are homologous appendages to the "leaf" portion of the angiosperm carpel; but, relative to conifers and *Ginkgo*, this homology would be simply a shared plesiomorphy of *Caytonia* and *angiosperms*, with independent infolding of the bract to envelop the seeds in the two groups. Our results suggest such possible broad homologies of strobilus organization, but also, because of the position of *Caytonia* and glossopterids, argue that carpels in angiosperms are homologous with the cupule/seed complex of *Caytonia* at the same level as the bract-ovuliferous scale complex of conifers.

It is interesting to note that the results obtained here for relationships within conifers are considerably different from those obtained by either Hart (1987) or Miller (1988). Most notable is the placement of Podocarpaceae and/or Cephalotaxaceae as the first branch of the conifer clade in our analyses, in contrast to the basal position of Taxaceae (Miller, 1988) or Pinaceae (Hart, 1987) in other analyses. On the other hand, it is interesting that the Podocarpaceae, Cephalotaxaceae, and Taxaceae are the first three branches, respectively, in our results. Historically, systematists have suggested in one way or another relationships between these three families, but without synapomorphies to unite them. A plesiomorphic assemblage perhaps best expresses this situation.

The position of *Callistophyton* in all of our analyses that include fossils was consistently below the "ginkgophyte" clade, including the Permian–Mesozoic seed ferns, and "above" the cycads, lyginopterids, and medullosans. We did not find a close association of *Callistophyton* with the conifer clade, as has been proposed by some authors (e.g., Rothwell, 1982). However, some characters shared by Mesozoic seed ferns and at least some conifers may represent shared plesiomorphies retained from a callistophytalean-like ancestor; this is consistent with numerous of the trees found in our complete analysis.

The intent of our analyses has not been to evaluate patterns within angiosperms, and our sample is insufficient to make any firm conclusions about phylogeny within the angiosperm clade. Whether or not our sample within angiosperms has been sufficient to stabilize the placement of angiosperms relative to other seed plants remains to be seen, as discussed below. We consider our results to be more an indication of the preliminary nature of all seed plant/angiosperm analyses up to this point, and expect numerous differences from our results within angiosperms in future analyses. Certainly, additional characters need to be included to provide greater resolution within angiosperms, which may also affect the relationships of the angiosperm clade to outgroups and outgroups to each other.

Over the past century, much emphasis has been placed on the question of which modern angiosperms most closely resemble the "ancestral" angiosperm (e.g., Arber & Parkin, 1907; Cronquist, 1981). In more recent cladistic studies, emphasis has been placed on determining the "first branch" of the angiosperms. While such questions have immediate appeal, it should be pointed out that: (1) the first, or "ancestral," member of any monophyletic group did not necessarily resemble the extant lineage of the "first branch" (sister clade of the remainder of the group), because of autapomorphic features developed since the time of divergence; (2) the concept of "first branch" is itself confounded, since the sister group of the "first branch" is equally the "first branch." It is probably preferable to refer to such "first" or "basal" branches as "one of the basal branches" or "most plesiomorphic terminal" but unfortunately, such terminology is unwieldy.

If the gnetopsid group is paraphyletic relative to the angiosperms, then our best estimate of the primitive angiosperm will still be affected by parsimony analysis within angiosperms. Unfortunately, the popular notion that we can estimate the ancestral state of a group by inference, if we know the topology of outgroup taxa, is erroneous (Nixon & Carpenter, in press) and has been based at least in part on misinterpretation of Maddison et al. (1984). Likewise, the ingroup topology of the angiosperm clade, and which angiosperm taxa are sampled, will affect the topology of outgroups; thus, we hope that methods of compartmentalization (e.g., Maddison et al., 1984) will be replaced by broader sampling within groups and simultaneous analysis of ingroup and outgroup pattern. How to determine when samples are of sufficient breadth to produce reliable and stable results is still an area of active research.

Using DADA, constrained analyses were input to Hennig86; with DADA, taxa can be constrained to be grouped into certain topologies, but taxa may also be allowed to "float" by assigning ambiguous group membership variables. When the cycads were constrained to form a monophyletic group with gnetopsids and angiosperms, but allowing the pteridosperms to "float" (not constrained, either inside or outside of the group), for the complete data set, the tree was two steps longer. When the topology was constrained to the results of Doyle & Donoghue

(e.g., 1992) for cycads and anthophytes (monophyletic gnetopsids, *Pentoxylon* part of gnetopsid clade, these two a sister group to a monophyletic Bennettitales), the trees are at least 16 steps longer. If the pteridosperms are allowed to "float" in such trees, surprisingly, they are a basal part of the *Ginkgo*–conifer clade in all most parsimonious trees; if they are constrained within the cycad–anthophyte assemblage, the trees are even longer than 16 steps, depending on the extent to which the analysis is constrained. Successive weighting of the complete matrix (Hennig86, xsteps w command) results in two trees; *Ginkgo* is placed outside of the conifer–anthophyte group in both these trees. The trees differ only in placement of Cephalotaxaceae and Podocarpaceae as alternative basal branches within the conifer clade. The trees are similar to those found in analysis IV (angiosperms condensed to a single terminal), with *Pentoxylon* subtending the anthophyte clade, and glossopterids and *Caytonia* forming a monophyletic group below the "ginkgophyte" clade.

THEORETICAL ASPECTS

The results of various manipulations of our data matrix, by excluding or including fossil taxa, and fusing multiple taxa into single terminals, have several broader implications for these types of analyses. It is clear that sample size and distribution of taxa are extremely important. Compartmentalization (by treating diverse taxa as single polymorphic terminals) may result in very different results, even if the compartmentalized group is monophyletic in all uncompartmentalized analyses (e.g., the angiosperms in our analyses). These phenomena are independent of what the "correct" phylogeny may be; the fact that such changes in results occur is of interest outside of whether one or the other solution is "more" correct. When the angiosperms are treated as a single polymorphic terminal, allowing *more* possible combinations to be basal within the angiosperms, fewer topologies are found outside of the angiosperms (e.g., *Pentoxylon* always basal to the anthophyte clade, in contrast to the unresolved position of *Pentoxylon*) than when the component angiosperm taxa are sampled. While this might seem counterintuitive, it is consistent with the effects of ambiguity and polymorphism reported by Nixon & Davis (1991). Thus, scoring a taxon as polymorphic does not necessarily allow more possibilities for its relationship to other taxa, and likewise does not result in predictable loss of overall resolution. The internal combinations of polymorphisms themselves either restrict or expand the possibilities for both ingroup and outgroup topologies, in ways that appear to be tractable only through observation of ingroup variation and breaking up of ingroup taxa into monothetic units.

UNDERSAMPLING

Undersampling of any pattern that is not perfectly hierarchic will in general result in increased levels of hierarchy in the data, potentially resulting in false hierarchy (see Nixon & Wheeler, 1991). Homoplasy in cladograms (error, e.g., the inability to distinguish homology from nonhomology) results in deviation from perfect hierarchic structure; the greater the level of homoplasy, the greater the problem of false hierarchy associated with undersampling. In broad analyses of the type undertaken here, homoplasy may be due to an inability to distinguish parallel or otherwise independent origins of structures, or inability to see that two structures are actually homologous; in all cases, homoplasy should not be considered something that occurs in nature, but instead is simply error in the interpretation of characters (the concepts of parallelism and convergence refer to evolutionary *interpretations* of homoplasy). Of necessity, our analyses, like other previous analyses, suffer from this problem, particularly in our limited sample of angiosperm taxa. Unfortunately, within angiosperms, we feel that it is not possible at this time to summarize character distributions for large groups of taxa, since at this point there is very little consensus among the results of phylogenetic analyses, most of which suffer from the very problems that we have discussed here. Thus, we anticipate that as additional angiosperm taxa are added, patterns may change and eventually stabilize on particular patterns, both within and outside of the angiosperms, when samples become sufficient. It is impossible at this point to predict what adequate sample sizes may be.

MISSING DATA

There can be little doubt that missing data introduce uncertainty into cladistic analysis, but to date there is no method to measure such uncertainty, nor to predict its effects. A widely held belief (from our experience with students and colleagues), is that missing data will merely increase the number of equally parsimonious solutions but that the solution will still include the shortest trees that would be found if missing data were known. This is definitely not the case (Nixon, in prep.; see also Nixon & Davis, 1991), and is related to the problem of

undersampling and homoplasy discussed above. Thus, if there is no homoplasy in the data, substituting missing data for real data will only result in less resolved trees, the strict consensus of which will not be in conflict with the original trees based on full data sets. However, with greater levels of homoplasy, increasing levels of missing data increase the likelihood that some or *all* trees found may be in conflict with the original trees. In extreme examples, the original trees may not be found at all. This can be extrapolated from the examples for polymorphism (ambiguity) illustrated by Nixon & Davis (1991). Specific patterns within groups (restricting the states for basal groups), when considered ambiguous, may actually *restrict* the equally parsimonious solutions, by allowing the terminal to join another clade that reduces homoplasy in other characters that have been scored properly. The problem of homoplasy interacting with missing data is thus severe, and we have not escaped it in our analyses, which have levels of missing data varying from 8 to 24% and consistency indices in the range of 0.39–0.79. The other aspect of this problem which has not been explored is the nature of ambiguity in the data; for instance, we scored several characters that are known only within angiosperms (e.g., floral characters) as nonapplicable (represented by a dash in Table 1) for non-angiosperms. Because the angiosperms are monophyletic in all analyses, such missing data will not have the kinds of effects outside the angiosperms that dispersed missing values will have when they actually contribute to placement of taxa. This area needs further investigation, and perhaps characters scored as inapplicable when all applicable scores form a monophyletic group should be reported separately from other kinds of ambiguity in the data.

Conclusions

Our analyses support the Loconte & Stevenson (1990) results in terms of the phylogenetic relationships of extant seed plants as (cycads (ginkgo conifers (gnetopsid–angiosperms))). This pattern is immutable throughout the various manipulations of our data. Thus, we reject the closer connection of cycads with the gnetopsid–angiosperm clade found in the studies of Doyle & Donoghue (1986a, b, 1987, 1992).

While our analyses are not definitive in regard to relationships of angiosperms to gnetopsids and Bennettitales, it is apparent that a closer relationship of angiosperms with the extant gnetopsids than has been proposed in recent studies must be considered, and the possibility that the "gnetopsid" group is paraphyletic bears close attention. Because of the major role that morphological analyses must play in any total evidence analysis, and because fossil data are largely restricted to morphology, our eventual understanding of the origin of angiosperms must be based on further, detailed comparative work among gnetopsids (and other seed plants) and a broad sample of angiosperms. Compartmentalized studies, at this point in time, will fail because the most parsimonious placement of any diverse group can only be determined by simultaneously including evidence of the structure of internal variation within the group. Compartmentalization has been applied directly by Donoghue & Doyle (1989) in their within-angiosperm analyses, which were based in part on previous results of seed plant analyses. Subsequently, Donoghue (1989) joined three separately produced cladograms for seed plants (Doyle & Donoghue, 1986b), basal angiosperms (Donoghue & Doyle, 1989), and conifers (Hart, 1987), and mapped characters such as "dioecy" onto the composite cladogram. These kinds of studies relax global parsimony, so that the "composite" cladograms are not guaranteed, nor, in our opinion, even likely, to be the most parsimonious topologies for the characters that are mapped. Additionally, the analysis by Donoghue (1989), built upon a previous analysis that had at least some unjustifiable character codings for the compartmentalized angiosperm taxon (e.g., alternate phyllotaxy, spiral microsporophylls, and others discussed above), and questionable codings for some taxa (e.g., "angiosperms") of the character (dioecy) under investigation. At present, when conflicting results are commonplace among and between data sets from a wide array of data sources, it seems premature to attempt to draw anything but very broad conclusions from these data. Any rush to map evolutionary scenarios onto existing cladograms seems rather futile.

Within angiosperms, *Chloranthus* and *Ceratophyllum* were the "first branches" in various of our analyses. In constrained analyses, a monophyletic gnetopsid group favors *Ceratophyllum* as a basal branch of the angiosperms (and vice versa), while *Chloranthus* as a basal branch favors a paraphyletic gnetopsid group (and vice versa). This, as well as numerous other examples in our data, illustrates the interdependency of subtree topology under the criterion of global parsimony. Such interdependency of clades may call into question not only compartmentalization but also clade support

statistics (e.g., the bootstrap or Bremer (1988) support; see also Donoghue et al., 1992), which attempt to measure reliability or confidence in particular branches of cladograms, in isolation from other branches. Individual branches within cladograms clearly are not independent events relative to the occurrence of other branches; trees occur as wholes, not isolated clades, and changes within one clade may have dramatic effects in other parts of the tree. With morphological data, new methods that are in development (Davis et al., 1993; Davis, 1993) may offer more useful ways of measuring quality of trees, as well as stability of clades; successive character removal, for example, identifies particular characters that are necessary for the support of particular groups, even when these characters do not change on the branch under consideration.

Finally, we urge readers to view our results only as a preliminary basis for examining a range of hypotheses about seed plant relationships. This range of hypotheses is somewhat broader than previous hypotheses for certain groups, we feel, because we have tied our data more directly to observed characters, as opposed to theoretically constructed terminals, for cycads, conifers, and angiosperms. Currently, most data on both fossil and extant seed plants are fragmentary, based on small samples, with low reliability and comparability across studies. The most important advances in our understanding of seed plant and angiosperm phylogeny will be made by careful comparative morphological and molecular studies that take into consideration the issues of sampling, taxon definition, and character coding that have such dramatic influence on the outcome of any cladistic analysis.

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Appendix A. Character list and discussion.

0. HABIT: woody (0); herbaceous (1); submerged-aquatic (2); additive.

Previous investigators (e.g., Loconte & Stevenson, 1990) have segregated shrub and tree habit (see character 0). We prefer to combine these two conditions as a single state "woody" because the distinction between tree and shrub is at best arbitrary, difficult in practice, and often polymorphic within angiosperm terminals. Woody is understood here to include a woody growth form derived from the presence of a bi-directional vascular cambium that produces secondary xylem centripetally and secondary phloem centrifugally. Consequently the monocots are not considered woody. However, the anomalous growth patterns of such taxa as the medullosans, *Pentoxylon*, and some cycads (Stevenson, 1990) are considered woody, because each of the "steles" in their stems does have a complete vascular cambium as described above and produces secondary wood that can be considered in terms of

wood anatomical features, as discussed below under wood anatomy. This is also applicable to the supernumery cambia that occur in some cycads as well as in *Gnetum*. The herbaceous and submerged aquatic growth habits are not known to occur in taxa in this analysis outside of the angiosperms. Logically, because all known submerged aquatics in our analyses are herbaceous (nonwoody), we have encoded character 0 as additive (ordered).

1. AXILLARY BUDS: absent (0); simple (1); multiple (2); additive.

Although this character is coded in terms of the presence of axillary buds, it is equivalent to the "branching dichotomous" versus "branching axillary" character of some previous analyses. The character is encoded as additive (ordered) under the assumption that multiple buds are derived. It should be noted that a nonadditive coding does not change our results. Dichotomous branching as used here includes both isotomous and anisotomous patterns. In some angiosperms, both axillary and dichotomous branching are known to occur in the same plant, but these instances are found in what we assume to be highly derived angiosperms such as some cacti (Troll, 1937; Boke, 1976) and some monocots (Fisher, 1973, 1976). Some cacti even have multiple buds in addition to dichotomous and axillary branching states (Troll, 1937). In all cases of dichotomous branching within the angiosperms, the taxa involved also express axillary branching in the same plants. All of the angiosperm terminals used in our analyses branch in axillary fashion.

Recently, it has been suggested by Doyle & Donoghue (1992) that dichotomous branching in extant cycads is derived from axillary branching. This conclusion is based upon the external morphology of the lower cretaceous fossil of the putative cycad *Nilssoniocladus* (Kimura & Sekido, 1975) and putative axillary branching in *Lyginopteris* and medullosans. In the case of *Lyginopteris*, the evidence that has been presented (Galtier & Holmes, 1982) is equivocal, and branching in *Lyginopteris* appears to be similar to the adventitious branching found on the petiole bases of extant dennstaediod ferns, based on position and vascular organization (Stevenson, 1974). In the case of the medullosans, only one species, *Medullosa endocentrica*, has been reported as having axillary branching (Hamer & Rothwell, 1988). This points to the problem of scoring reconstructions based on different form genera, and the problem of synthate taxa based on assumptions of relatedness. We have thus coded both our medullosan and lyginopterid terminals as uncertain (ambiguous) for the character of axillary branching.

According to Kimura & Sekido (1975), the inclusion of *Nilssoniocladus* within the cycads is based upon straight epidermal cell walls and the presence of haplocheilic stomata. Both of these characters are plesiomorphic within seed plants, based on several recent analyses as well as traditional concepts; therefore, the presence of these characters in a fossil cannot exclusively nor conclusively indicate cycadalean affinity. In fact, *Nilssoniocladus* has no synapomorphies with either extant or known extinct cycads. The short-shoot morphology and simple leaves of *Nilssoniocladus* are not known for extant cycads or any fossils that share synapomorphies with the cycads. There is no axillary branching evident in the earliest unequivocal cycads, *Crossozamia chinensis* Zhu & Du and *Tianbaolinia circinalis* Gau & Thomas from the Early Permian of China (Gao & Thomas, 1989), which are virtually indistinguishable from the extant genus *Cycas*. Because we find no evidence to support axillary branching as occurring in either fossil or extant cycads (Stevenson, 1988), we have maintained the position of Loconte and Stevenson and scored all cycad taxa as lacking axillary buds (state 0).

2. SHORT SHOOTS: absent (0); present (1).

Short shoots are defined as lateral shoots that differ in morphology from main shoots by suppression/reduction of internodes (as in *Ginkgo*).

3. APICAL MERISTEM: w/o tunica (0); w/tunica (1).

The concept of tunica-corpus organization of shoot apical meristems has been discussed by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). The character as treated here is equivalent. However, as discussed by Loconte & Stevenson (1990) we consider the corpus and the lack of a tunica to be vascular plant plesiomorphies and the presence of a tunica to be apomorphic. The plesiomorphic presence of the corpus in the seed plants is not a semantic issue as suggested by Doyle & Donoghue (1992). Rather, it is a necessary part of the stem apical growth in the seed plants, and its presence is supported not only by histology but also by cytohistochemistry and cell division patterns in terms of maintaining the conical shape of the meristem (Gifford & Corson, 1971; Steeves & Sussex, 1989).

4. STELE: protostele (0); eustele (1); polystele (2); nonadditive.

The common condition throughout extant seed plant groups is eustelar organization. Among the terminals used in our analyses, *Ceratophyllum* has a protostele, as found in many (apparently unrelated) submerged aquatic angiosperms such as *Mayaca*. Given the probable phylogenetic position of these taxa, the protostelic condition of certain aquatic angiosperms is almost certainly derived from the eustelic condition. Some members of the Cycadales have a polystelic condition similar to that found in many medullosans (Stevenson, 1990). We have also scored *Pentoxylon* as having a polystele although it differs from that found in the cycads and medullosans in anatomical details (see sections on fossil groups).

5. NODAL ANATOMY: 1-trace unilacunar (0); 1-trace per bundle (1); multilacunar (2); 2-trace unilacunar (3); trilacunar (4); nonadditive.

Nodal anatomy is scored as in Loconte & Stevenson (1990). This character as scored in Doyle & Donoghue (1992) is a composite character of petiole anatomy and nodal anatomy and as such excludes certain possible combinations. This would be particularly true if one were to include ferns in an analysis. This character should be limited to the number of departing traces as related to the number of supplying bundles in the stem. For example, Doyle & Donoghue (1992) considered that cycads have a number of traces derived from a solid arc of xylem. Our observations do not confirm this. The leaf trace system of cycads is derived from numerous small bundles that only appear as a solid arc after the production of secondary xylem has obscured the integrity of the primary vascular system (Chamberlain, 1935). We have therefore scored all three cycad terminals as state 2 (multilacunar). In contrast, the vascular pattern of the petiole in cycads reflects the division of bundles in the cortex of the stem.

Thus, the number of bundles departing from those of the stem is not directly related to the number or arrangement in the petiole. In fact, the number of departing traces does not even represent a minimum number because of anastomoses that may occur in the cortex. Also, the anatomy of departing traces does not necessarily match that of the leaf traces (see discussion under character 24—leaf trace xylem).

6. GIRDLING LEAF TRACES: absent (0); present (1).

Girdling leaf traces (with multilacunar nodal anatomy) are known only from the extant and fossil Cycadales, and thus this character is a synapomorphy for the Cycadaceae, Stangeriaceae, and Zamiaceae (Stevenson, 1990).

7. PRIMARY XYLEM: mesarch (0); endarch (1).

Primary xylem character (7, 8) states are described for fossil taxa under those entries. All of the extant taxa in this study have endarch primary xylem (character 7).

8. PRIMARY XYLEM PITS: scalariform (0); conifer type (1).

This character is the same as used in Doyle & Donoghue (1992) and various previous analyses; data are derived in large part from Greguss (1955) and Bierhorst (1971).

9. WOOD: manoxylic (0); pycnoxylic (1).

Basically the same as used by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Data for manoxylic versus pycnoxylic xylem are derived from Greguss (1955) and descriptions of fossil taxa in the literature (see Stewart & Rothwell, 1993; Taylor & Taylor, 1993, and references cited therein).

10. SECONDARY XYLEM PITS: scalariform (0); mixed (1); circular (2); additive.

Secondary xylem pitting is considered to refer only to the lateral walls of the tracheary elements of the secondary xylem and is treated as an additive multistate character. The state "mixed" refers to the presence of individual tracheary elements that have both scalariform and circular pits. We have scored this as an additive character to avoid problems of the polymorphic "mixed" condition. The additivity of the character is consistent with allowing a polymorphic stage to be intermediate between two endpoints; it also maintains grouping information that is lost if "mixed" is scored as an independent state in a nonadditive character. Of course, the co-occurrence of both circular and scalariform pits suggests that, while there may be ecological and/or conceptual reasons to associate these in the same character, they may be independent characters. Because there are no terminals that lack both scalariform and circular pits, treating this character as we have above is logically and computationally identical to scoring two separate binary presence-absence characters for scalariform and circular pits.

11. XYLEM RAYS: uniseriate/biseriate (0); some multiseriate (1).

Basically the same as used by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Data are derived mostly from Greguss (1955) and descriptions of fossil taxa in the literature (see Stewart & Rothwell, 1993; Taylor & Taylor, 1993; and references cited therein). Some data are also derived from standard wood references such as Brown & Panshin (1934).

12. VESSELS: absent (0); present (1).

In order to reduce bias due to preconceived notions about the evolution of vessel elements (in particular perforation plates), we have separated the form of the perforation plate (character 13) from whether or not vessels occur. This assumes that angiosperms (scalariform) and gnetopsid (foraminate) vessels are homologous; see Muhammad & Sattler (1982) for a discussion of the similarity of gnetopsid and angiosperm vessel elements.

13. VESSEL PERFORATIONS: foraminate (0); scalariform (1).

See Muhammad & Sattler (1982) for a discussion of this character in *Gnetum*. The simple perforations of some angiosperms (e.g., *Chrysolepis*) were assumed to be derived from, and therefore were scored as, scalariform. Adding the third state "simple" would provide little if any grouping information in our analyses, but would be useful in an expanded analysis that included more angiosperms.

14. SIEVE TUBE PLASTIDS: s-type (0); p-type (1).

As used in numerous previous analyses. We were not able to utilize subclasses of the two types of plastids. Data are from Behnke (1988) and references cited therein.

15. COMPANION CELLS: absent (0); present (1).

As defined by Loconte & Stevenson (1990) and Doyle & Donoghue (e.g., 1992).

16. LIGNIN SUBUNITS: vanillin (0); syringal groups (1).

Data for vanillin versus syringal subunits of lignin are from Logan & Thomas (1985). Only known for extants; the chemical assay of lignin type (Mäule reaction) requires intact wood.

17. CORTICAL SECRETORY STRUCTS: absent (0); cavities (1); canals (2); nonadditive.

Data are from Bierhorst (1971), Taylor & Taylor (1993), and from unpublished observations. Secretory cavities are areas in parenchymatous tissue where there are independent lacunae that are lined with secretory epithelial cells. In contrast, secretory canals are longitudinal structures that form a network of lacunae that are lined with epithelial cells. In both cases, the lacunae are schizo-lysigenous in origin. Cortical secretory structures vary independently from secretory structures that often occur in secondary xylem or rays. Thus, taxodiaceous and cupressaceous mature woods lack secretory canals, but canals are present in the cortical tissues of young stems. This three-state character has been treated as unordered because there is no direct evidence that canals are derived from cavities.

18. ETHEREAL OIL CELLS: absent (0); present (1).

Ethereal oil cells (as far as known) are limited to angiosperms. The cells that produce ethereal oils are specialized parenchyma cells. Data are from Cronquist (1981).

Loconte & Stevenson (1991), and general taxonomic references.

19. RESINS: absent (0); present (1).

Although resins are the products of secretory structures, there is not a one-to-one correlation between type of secretory structure (e.g., canal or cavity) and the type of secretion (e.g., resin or mucilage). The presence of these resins is limited in seed plants to extant and extinct conifers (but conspicuously absent from cordaitalean taxa) and corystosperms. It should be noted that while conifers have resin-secreting canals, the corystosperms have resin-secreting cavities (dealt with in character 18). In the same manner, the cycads, medullosans, and cycadeoids have non-resin secreting canals (mucilage in the cycads), whereas *Ginkgo*, *Callistophyton*, *Lepidopteris*, *Tatarina*, and *Glossopteris* have secretory cavities that do not produce resins (at least these have not been detected in the above fossils).

20. PHYLLOTAXY: alternate (0); opposite or whorled (1).

Phyllotaxy is treated as either alternate or opposite/whorled. As have previous workers, we have treated whorled leaves as a subset of opposite; such treatment is supported by the common association of the two states in disparate groups, as in the case of *Ephedra* where some species have opposite leaves and others have whorls of three leaves at each node. Pseudowhorls or pseudo-opposite phyllotaxy are often difficult to recognize, as is the case in *Catalpa* and *Peperomia* (Schoute, 1922, 1925). Of the taxa used in our analyses, perhaps the most problematic is *Platanus*, which we have scored as alternate (the traditional interpretation), but which may in fact be derived independently through sympodial branching and reduction of one leaf at each node to become the foliar "stipule" that encircles the stem, much as the leaf base encircles the axillary bud.

21. LEAF BASE: simple (0); sheathing (1).

Because of difficulty in scoring early developmental stages in fossil taxa, we have restricted our definition of "sheathing" leaf base to those taxa which express the condition in mature leaves. Thus, those taxa that appear to have sheathing leaves during early ontogeny such as in the cycads (Stevenson, 1990), but do not have sheathing leaves at leaf and stem maturity, are scored as having simple leaf bases.

22. STIPULES: absent (0); present (1).

Stipules are considered here to be the presence of appendages associated with the leaf base. These may be borne on the leaf base, petiole, or adjacent parts of the stem. The character is limited in distribution to some angiosperms and some cycads (Stevenson, 1990). Because of the diverse nature of these structures, it is unlikely that all stipules are homologous; the character has been retained here only tentatively until more detailed comparative analyses of "stipular" structures can be developed.

23. LEAF TRACE XYLEM: mesarch (0); endarch (1).

We have introduced a new character dealing with endarch versus mesarch (including exarch) leaf traces. This character is not strictly correlated with the xylem pole position in stem bundles as might be supposed. For example, the cycads have endarch stem bundles with mesarch leaf traces (Stevenson, 1990).

24. LEAVES: simple (0); compound (1).

While a few fossil taxa are difficult to score, this is a fairly straightforward character.

25. PRIMARY VEIN FORM: dichotomous (0); anisotomous (1); solitary/unbranched (2); nonadditive.

This character refers to the primary vein system only, and thus avoids the problem of scoring "midvein dichotomous" in one taxon, and midvein "not dichotomous" in taxa such as *Ginkgo* with only one order of veins.

26. LEAF VENATION: parallel (0); pinnate (1); palmate (2); nonadditive.

This character was coded only for taxa with more than one order of venation, or in the case of parallel venation, those with multiple primary veins (e.g., *Ephedra*). Taxa such as conifers and *Ginkgo* were coded as inapplicable (−) because the primary vein form character adequately describes the leaf venation.

27. VEIN ORDERS: one (0); two (1); three or more (2); additive.

All taxa in our analyses have at least one order of venation. Two vein orders occur by branching off from the primary midvein (e.g., *Gnetum* and most angiosperms) or parallel primary veins (e.g., *Welwitschia* and monocots). This character was scored as additive because of the logical dependence of states 1 and 2 (if a leaf has three orders of veins, it by definition has two as well). Size classes of veins were used, and the rachis of certain compound leaves was considered to be the "primary" vein (as was implicit in the codings of some leaf characters in Doyle & Donoghue, 1986a, b, 1987).

28. LAMINAR VEIN FORM: dichotomous (0); anisotomous/non-dichotomous (1).

Laminar vein form refers to the pattern of venation in leaves with more than one order of veins; it is not scored (inapplicable) in those taxa with only one order of veins (e.g., *Ginkgo*) because the form of the primary vein in such taxa has already been described in character 25. Based upon developmental studies (Rodin, 1967) it is clear that *Gnetum* has an angiosperm-like venation pattern based upon a system of anisotomous branching rather than the common monopodial pattern of the angiosperms.

29. VEIN FUSION: nonanastomosing (0); anastomosing (1).

Vein fusions occur in those forms that are dichotomous and anastomosing (e.g., *Encephalartos* and *Gnetum*) as well as nondichotomous anastomosing forms in angiosperms. In some taxa, anastomoses occur only near the margins of leaves (e.g., *Ginkgo*) and do not occur consistently throughout the lamina. In such cases, the taxa were scored as nonanastomosing because the anastomoses are not consistent throughout the lamina or from leaf to leaf. The character therefore is defined as anastomoses consistently distributed over the leaf blade.

30. CHLORANTHOID TEETH: absent (0); present (1).

This character has been used in previous within-angiosperm analyses (e.g., Donoghue & Doyle, 1989). We note, however, that in that analysis assumptions were made about plesiomorphic states within the "hamamelid" terminal.

31. GUARD CELL POLES: raised (0); level (1).

This character and character 32 have been used routinely in seed plant analyses (e.g., Crane, 1985; Doyle & Donoghue, 1987, 1992; Loconte & Stevenson, 1990). We note that it is difficult to determine with certainty in some fossil material.

32. STOMATES: haplocheilic (0); some or all syndetocheilic (1).

See Doyle & Donoghue (e.g., 1987).

33. ASTROSCLEREIDS IN LEAF: absent (0); present (1).

The definition and scoring of this character follows that of Loconte & Stevenson (1991).

34. STROBILI: unisexual (0); bisexual (1); functionally unisexual (2); additive.

This character refers to the sex of whole strobilar axes. By definition, all dioecious plants are unisexual, regardless of the interpretation of what constitutes a strobilus. Scoring of some taxa is of necessity dependent on the interpretation of "strobilus" but in practice there seems to be little difficulty, and our interpretations are generally consistent with previous analyses. The angiosperm flower is here considered to represent a bisexual strobilus. Under the assumption that functionally unisexual strobili with vestigial parts of one sex (e.g., fertile microsporophylls and a sterile ovule, as in *Welwitschia*) are derived from bisexual axes, we have encoded this character as additive.

35. PERIANTH: absent (0); present (1).

The perianth is here operationally defined as a set (whorl or spiral) of sterile appendages subtending carpels and/or stamens; because of uncertain homology we have not scored the gnetopsids or cycadeoids as possessing a perianth. The bracts subtending the strobilus of cycadeoids, while prominent, are no more definitively homologous to the angiosperm "perianth" than are the often sterile bracts in the lowermost portion of the strobili of some Pinaceae. Until more certain homology of reproductive structures of gnetopsids, angiosperms, and cycadeoids can be postulated, it seems unwise to declare homology in some parts of the "strobili" when positional relations of parts are unknown; characters such as "perianth" are homologous only by their positional relation to carpels, which are unknown (or unrecognized) outside of the angiosperms.

36. MICROSPOROPHYLL: pinnate (0); simple (1).

We interpreted angiospermous stamens as microsporophylls; there is a long history of other interpretations (e.g., such as diphyllous structures, peltate structures; see Eames, 1961). In general, outside the angiosperms, microsporophylls were interpreted as planate or laminar structures to which microsporangia (or synangia) are attached. Our interpretations have in general followed traditional lines. In those cases where the attachment and nature of pollen-bearing organs is uncertain (e.g., medullosans) these characters are scored as ambiguous (see also section on medullosans).

Based upon the extensive studies of Martens (1971, and literature cited therein), *Ephedra* and *Welwitschia* are scored as having pinnate microsporophylls instead of simple microsporophylls as they have been scored in some previous analyses. In *Welwitschia*, the six "simple" microsporophylls (as interpreted by Doyle & Donoghue, 1986a, b, 1987, 1992) are supplied by two vascular traces, each of which branches to supply three "simple" appendages (Sykes, 1910). Each of these groups of three are characterized by a larger appendage (the central one) and two smaller lateral appendages; in early stages of development (Martens, 1971) these can be clearly seen as two opposite three-lobed structures; further evidence that these are indeed two opposite structures is found in their position relative to subtending bracts, which are decussate; if interpreted as two opposite three-lobed structures, the microsporophylls continue perfectly the decussate taxis of the strobilus; this taxis then continues *above* the two microsporophylls in the two sterile bracts enveloping the sterile central ovule (Martens, 1971). The clearly oppositely arranged three-pinnate microsporophylls of *Welwitschia* have been widely interpreted as six simple sporophylls that are basally fused (e.g., Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992). Likewise, the evidence is strong that microsporophylls of *Ephedra* are opposite or whorled compound (pinnate) structures that are partially or completely fused. *Gnetum* appears to have opposite, connate simple sporophylls; an obvious interpretation is that these are reduced from compound sporophylls of a cycadeoid or *Welwitschia* type.

Within angiosperms, we have followed tradition and encoded all taxa as having simple microsporophylls; however, it is worth pointing out that *Chloranthus* might as easily be interpreted as having (in some species) three-lobed pinnate microsporophylls as opposed to the traditional interpretation that these are three simple stamens that have migrated together, become fused, and the two lateral ones are reduced in size (see Herendeen et al., 1993 for a discussion of the various interpretations of *Chloranthus* stamens and their implications). If the chloranthoid stamens are interpreted as compound pinnate structures, the reduced lateral "glands" found at the base of many Lauralean stamens might also be interpreted as reduced lateral pinnae of a chloranthoid pinnate microsporophyll. We have not encoded any such interpretations in our matrix, but hope that further investigation of angiosperm taxa as well as gnetopsids may provide evidence to support or refute the existence of pinnate microsporophylls within angiosperms. Certainly the presence of pinnate microsporophylls in both commonly accepted outgroups to angiosperms (cycadeoids and gnetopsids) makes the existence of pinnate structures in angiosperms, if not likely, at least not surprising.

37. MICROSPOROPHYLLS: spiral (0); whorled/opposite (1).

This is a straightforward character, except in certain fossil groups such as the glossopterids (due to missing parts or difficulty in determining homology). It should be noted that in Doyle & Donoghue (1986a, b, 1987, 1992), the single angiosperm terminal was scored as having spiral

microsporophylls; in our analysis, by scoring numerous angiosperm taxa as observed, we allow parsimony to select the likely ancestral state for angiosperms.

38. MICROSPOROPHYLLS: free (0); basally fused (1).

This is a difficult character to score within angiosperms in some cases, particularly when fusion of parts such as the calyx and carpels may envelop the basal portion of stamens.

39. MICROSPORANGIA PER UNIT: many (0); 1–4 (1).

This character refers to the number of microsporangia per ultimate appendage, or sporangia-bearing "unit." This means that taxa such as medullosans can be scored because detached pollen organs provide at least a minimum number.

40. MICROSPORANGIA: terminal (0); marginal (1); adaxial (2); abaxial (3); nonadditive.

This character is similar in definition and scoring to one used in previous seed plant analyses; we note some difficulty in interpreting angiosperm taxa when the stamen form is filamentous and there is not a clear development of a connective extension (in our analyses, few such taxa were included, but with expanded analyses, this may pose a problem). The "peltate" theory for the origin of the angiosperm stamen (see Eames, 1961) is also germane to this character, for, if such an interpretation is accepted, then all angiosperm stamens are basically terminal (as in gnetopsids) and are modified developmentally to be marginal, abaxial, etc. We stand neutral on this issue, and prefer to score the character based on observation, not models of evolutionary transformation.

41. MICROSPORANGIA: free (0); fused at least basally (1).

This character is defined in the same manner as previous analyses; we find it difficult to score with certainty in numerous taxa, and our matrix reflects this.

42. MICROSPORANGIAL DEHISCENCE: ectokinetic (0); endokinetic (1); endothecial (2); nonadditive.

The concept of ectokinetic versus endokinetic microsporangial dehiscence was first introduced by Jeffrey & Torrey (1916). The ectokinetic mechanism is derived from epidermal cells, as in cycads, whereas the endokinetic system is derived from two or more subepidermal cell layers without epidermal differentiation, as in *Ginkgo*. We have introduced this character here and added a further state, endothecial, which is a subset of endokinetic, that utilizes only one subepidermal layer, the hypodermal layer. Scoring is based upon observations of extant and fossil taxa (Stevenson, unpublished). Further data are from Singh (1978) for many conifers and Martens (1971) for many gnetopsids.

43. MICROSPORE (POLLEN) SYMMETRY: radial (0); bilateral (1).

Pollen symmetry has been used previously; it is relatively straightforward, although in some instances the collapse of globose radial grains could produce a bilateral-appearing grain. Thus, all scores are based upon uncollapsed grains.

44. MICROSPORE TETRAD SCAR: present (0); absent (1).

Tetrad scars (character 47) are found only in fossil taxa in our analyses and the character is discussed under those entries. It is interesting to note that medullosans have both a proximal tetrad scar and a distal aperture; this supports the distinction between characters of the aperture and the tetrad scar.

45. MICROSPORE APERTURES: inaperturate (0); polar monoaperturate (1); equatorial multiaperturate (2); nonadditive.

This character has been used in some form in previous analyses; by scoring several angiosperms, we have not presumed their ancestral state. State 2, "equatorial multiaperturate," encompasses mostly triaperturate (tricolpate and tricolporate) taxa. Within angiosperms, character 47 below deals with variation within the tricolpate/tricolporate/triporate forms.

46. LEPTOMATE APERTURE: absent (0); present (1).

The "leptoma" is a distal rather indistinct germination pore (thin area in the wall) found in Cordaitalean and extant conifer pollen; it is more radially symmetrical in shape than the typical elongate sulcus of most monosulcate pollen.

47. COLPUS FORM: colpate (0); colporate (1); pororate (2); additive.

This character is scored as additive based on the compound nature of the apertures in the tripororate taxa included in our analyses (e.g., *Betula*). All monoaperturate and inaperturate pollen is scored as inapplicable to avoid unjustified weighting of the equatorial/multiaperturate character.

48. POLLEN SACCUS: non-saccate (0); saccate (1).

This character has been used in all previous seed plant analyses in a similar manner. See also character 49.

49. SACCUS FORM: eusaccate (0); quasisaccate (1).

Pedersen & Friis (1986) observed a denser, infilled (endoreticulate) saccus interior, or "quasisaccate" condition, in pollen of *Caytonanthus*; similar pollen is attributed to glossopterids and corystosperms (Taylor & Taylor, 1993). This may indicate multiple origins of saccate pollen or transformations within homologous saccate pollen types.

50. EKTEXINE STRUCTURE: alveolar or ramifying (0); granular/columellate (1).

Some variant of this character has been widely used in previous analyses. Because of difficulty in distinguishing categories of alveolar, honeycomb, ramifying, and various "solid" types of pollen, as well as a very confounded and inconsistent literature, we have chosen to lump ektexine structure for all of those putatively "primitive" types and differentiate only the granular/columellate forms as found in cycadeoids, gnetopsids, and angiosperms.

51. ENDEXINE STRUCTURE: lamellate (0); granular (1).

Previously used in seed plant analysis; our coding follows those. We should point out, however, that while all angiosperms are coded as having granular endexine, layered endexine is known especially in the zone of apertures, and perhaps this character needs to be reevaluated to take this into account.

52. TECTUM: absent (0); clearly defined (1).

As we define the tectum, it is a clearly consolidated outer layer of the ektexine; thus, we do not consider the loosely associated outer granular layer of some coniferophyte pollen to be tectate.

53. TECTUM STRUCTURE: columellate (0); granular or solid (1).

For those taxa that have tectate pollen, we have scored whether the tectum is underlain by columellae or granular/solid structure. In the case of *Betula* and *Casuarina*, we scored the granular/columellate wall as columellate.

54. TECTUM FORM: continuous or foveolate (0); semitectate or reticulate (1).

Scored only for tectate pollens. Terminology follows that of Walker & Doyle (1975).

55. PARALLEL EXINE STRIATION: absent (0); global (1); proximal (2); nonadditive.

Gross similarity in exine morphology has been noted between the glossopterids and *Ephedra* and *Welwitschia*; the "parallel" exine striations of these taxa, however, differ in their distribution and orientation (globally distributed in the gnetopsids and restricted to the cappus in glossopterids). Various striate pollen types of some angiosperms are not considered homologous with either of these types that are fundamentally supratectal in nature, although some taxa of striate angiosperms (e.g., certain Lauraceae) need investigation.

56. MICROGAMETOPHYTE: more than 4-nucleate (0); 4-nucleate (1); 3-nucleate (2); additive.

This character has been widely used in seed plant analyses; we encode it as additive under the assumption that reduced 4- and 3-nucleate types are part of a reduction series; other arguments for additive coding can be made on the basis of meristic logic.

57. POLLEN TUBE: suspended (0); penetrating (1).

The differences and significance of penetrating versus suspended pollen tubes are discussed in Loconte & Stevenson (1990). This character would appear to be correlated with motile versus nonmotile male gametes, as pointed out by Doyle & Donoghue (1992), but the latter is only known for extant taxa, and thus complete correlation is not known. The presence or absence of flagellate male gametes as dependent upon the presence or absence of penetrating pollen tubes is not necessarily dependent upon the latter just as ramiform pollen tubes are not dependent upon gamete motility.

58. RAMIFORM POLLEN TUBES: absent (0); present (1).

Ramiform pollen tubes occur in cycads, *Ginkgo*, and conifers but are not known in gnetopsids. With the exception of *Callistophytales*, the nature of pollen tubes is not known in fossil seed plants. Within angiosperms, branched pollen tubes appear to be correlated with chalazogamy in some hamamelidid groups (Eames, 1961); however, these data are spotty and inconsistent.

59. STALK CELL: present (0); absent (1).

The stalk cell is the sterile derivative of the antheridial cell in the male gametophyte (Singh, 1978). As pointed out by Singh, this cell should probably be called the "secondary prothallial cell," but historical usage is retained here. A stalk cell is found in the endosporic microgametophyte of the vascular cryptograms, cycads, conifers, and *Ephedra* (Singh, 1978). We have scored this character as unknown for all fossils, although the form of the male gametophyte in fossil Callistophytaceae (Millay & Eggert, 1974) indicates that it is probably present in this group.

60. SPERM: flagellate (0); nonflagellate (1).

All vascular cryptograms have flagellate sperm. In extant seed plants, flagellate sperm that are structurally more complex than those of cryptogams occur in cycads and *Ginkgo*. The remainder of extant seed plants are nonflagellate, and their nonmotile sperm are sometimes referred to simply as "male cells" (e.g., Singh, 1978). Lack of preservation prevents scoring this character for fossil taxa.

61. SIMPLE MEGASTROBILUS: absent (0); present (1).

62. COMPOUND MEGASTROBILUS: absent (0); present (1).

Characters 61 and 62 are logically connected, since all compound strobili by definition are made up of simple strobili; by separating the two components, we were able to code certain fossil taxa (e.g., *Caytonia*) as having *at least* simple strobili (determinate reproductive axes) without making decisions on how these detached organs might have been organized into compound axes. We define strobilus in this context as a determinate reproductive axis bearing fertile appendages; a "compound" strobilus is mostly a matter of branching order. With the exception of our reinterpretation of certain fossils (e.g., *Caytonia* and *Corsytosperms*) our scoring of this character is similar to that of previous analyses.

Cycas, with its alternating production of ovule-bearing structures with vegetative leaves on the same axis, does not have strobilar structure, and therefore is scored as lacking a simple megastrobilus. Medullosans, *Lyginopteris*, *Archaeopteris*, and *Callistophyton* are considered not to have a simple megastrobilus because the ovule-bearing structures are produced on what appear to be indeterminate stems in a manner similar to *Cycas* (see section on fossil taxa).

In some taxa that have a simple megastrobilus, e.g., Taxaceae, it is not clear if a compound strobilus is present, and such taxa have been scored as ambiguous. The work of Eames (1952), Martens (1971), Takaso (1984, 1985), and Takaso & Bouman (1986) clearly demonstrates the presence of a compound strobilus in the gnetopsids.

The "compound" nature of the microstrobilus of gne-

topsids might be considered a synapomorphy of the gnetopsid clade. We have not encoded a character for simple versus compound microstrobilus (as suggested by one anonymous reviewer). Given the uncertainty in interpretation of angiosperm floral homology, it is not possible to score angiosperm "microstrobili" (flowers) as unambiguously compound or simple; moreover this character has no effect on our results, because, if the angiosperms are coded as uncertain (as they should be), it is equally parsimonious for gnetopsids to be monophyletic or paraphyletic to an angiosperm clade. Within the conifer clade, some taxa are problematic in regard to this character, and at least some species of *Podocarpus* have what have been interpreted as compound microstrobili (Wilde, 1944). Additionally, numerous fossil taxa in our analysis would be unknown for the microstrobilus character.

63. WOODY CONES: absent (0); present (1).

The presence or absence of woody cones is limited to three conifer families and Cordaitales.

64. COMPOUND CONE UNITS: many (0), few (1).

This character reflects the degree of branching in compound cones and is of value only within the conifer clade.

65. CARPEL: absent (0); present (1).

The term carpel is used here in the classical sense (Gifford & Foster, 1988) and is considered to be an angiosperm synapomorphy. The homology of this structure with any structures outside of the angiosperms is uncertain, as is the nature of the carpel itself. We therefore prefer to define it strictly as a structure enclosing the ovules, on which pollen germinates; this eliminates such structures as the seed envelope of *Caytonia*, since pollen has been detected within the micropyles of in situ *Caytonia* ovules.

66. SEEDS: absent (0); radiospermic (1); platyspermic (2); nonadditive.

This character is commonly and widely used in seed plant analyses and phylogenetic discussions; we note that it is exceedingly difficult to score in numerous taxa, particularly some fossils, but differences of opinion also exist for major extant groups (e.g., whether the angiosperms have radiospermic or platyspermic seeds). In fact, the concept of radiospermy versus platyspermy is in itself not well established or clear. For example, "platyspermy" can arise simply by compression of developing ovules by subtending structures. We feel that the character needs to be more clearly defined on the basis of seed structure, instead of shape; shape also changes, sometimes radically, during seed development, and this information is rarely available and even then is not known for the majority of fossil taxa. For extant taxa, we have used the internal arrangement of vascular bundles, and the early stages of development of ovules, when known.

Gnetopsids are scored as radiospermic because the ovules are morphologically, anatomically, and developmentally radiospermic. What appears to be a platyspermic condition in *Welwitschia* is the result of enclosing bracteoles that become flattened and winglike, and not because of a flattened ovule. *Cycas* is scored as polymorphic, based upon evidence presented in Stevenson (1990), but the radiospermic condition in this genus is still unresolved. Although the angiosperms in our analyses are scored as platyspermic, it is not clear whether the concept is applicable without ontogenetic studies across the spectrum of angiosperms.

67. OVULE POSITION: stalked (0); foliar (1); peltate/enclosed (2); nonadditive.

The angiosperms are scored as ambiguous for this character because of the homology of the carpel/placenta. Carpels may be simple leaf-homologues bearing seeds or may be compound structures that include a leaf homologue that subtends an axillary structure bearing seeds (much like a conifer bract/scale complex). It is interesting to note that both groups commonly referred to as sister taxa or outgroups of angiosperms (cycadeoids and gnetopsids) have ovules borne on stalks with no indication of foliar attachment; gnetopsids bear subtending bracts, and at least one interpretation of the sterile scales of cycadeoids is that these are bracts subtending ovules. Thus, a complex origin of the carpel from a leaf homologue/axillary stem seems likely based on outgroup comparison, extending all the way to the coniferophytes and *Ginkgo*.

The peltate/enclosed ovule position is found in the Mesozoic seedfern taxa, which have peltate or laminar/peltate structures that sometimes enfold the ovules. These structures are difficult to interpret as to whether they include both the lamina and axis. We hesitate to score these as homologous with angiosperm carpels for reasons outlined above.

68. OVULE NUMBER: 1–2 (0); many (1).

This character has been widely used in previous analyses in similar forms. Undoubtedly, the problem of foliar versus axial ovules makes it unlikely that such characters are homologous over all seed plants.

69. OVULES: orthotropous (0); anatropous (1).

This character has been used previously, but in our opinion has been improperly coded on the basis of phylogenetic hypotheses instead of on observed morphology in real taxa. We base our definitions of orthotropous and anatropous on the position of the funiculus (ovule stalk) of individual ovules, without assuming that associated structures or groups of ovules later become parts of solitary ovules. The two states are thus a straight ovule in line with the funiculus (orthotropous) or recurved ovule along the funiculus (anatropous). Thus, unlike Doyle & Donoghue (1986a, b, 1987, 1992), we have scored *Caytonia* as having orthotropous ovules. It is the structure that encloses the numerous ovules that is recurved in *Caytonia* (see discussion in fossil section).

70. MICROPYLE: normal (0); tubular (1).

The "normal" micropyle in this case refers to the case in which the inner integument is not elongated into a tube. This character bears further investigation within angiosperms, some of which have extended inner integuments that act as obturators.

71. MICROPYLE ORIENTATION: distal (0); proximal (1).

This character refers to the direction in which the ovule and micropyle point relative to the structure that bears the ovuliferous structure (e.g., axis of the strobilus). It is most useful for differentiating cycad and conifer reproductive structures (Crane, 1988; Stevenson, 1990).

72. OVULE GROWTH: pachychalazal (0); endochalazal (1).

Two contrasting states of ovule growth, pachychalazal and endochalazal, were introduced by Takaso & Bouman (1986). Because this character requires some knowledge of ovule development, it is only applicable at this time to extant groups. The character distinguishes those ovules that have a massive chalaza with integuments generally attached above the middle of the ovule. This is brought about because of unequal development of the chalaza and the integument in such a way as to give rise to a greater part of the seed from the chalazal end in pachychalazal ovules (Takaso & Bouman, 1986). In contrast, gnetopsids and angiosperms appear to have more of an integumentary development (the area above the integument attachment) and are termed endochalazal by Takaso & Bouman (1986). This latter term seems somewhat of a misnomer as the development does not truly occur within the chalazal portion.

73. OUTER SEED ENVELOPE: absent (0); present (1).

We have attempted to develop a character for various layers and/or appendages that envelop the ovule/seed that is less dependent on phylogenetic hypotheses in interpreting and encoding character states than in previous analyses. We thus define outer seed envelope as a layer that directly invests an individual ovule, in contact with the integument ("inner integument") and extending to the micropylar region. We are not convinced of the direct homology or lack of homology of various of these structures, but see no other way to encode such characters that does not bias the results toward particular interpretations. Thus, we have scored as equivalent the second integument of certain angiosperm ovules, the bracteoles of the gnetopsids, and other similar structures in fossil taxa. We have not included arils that are not completely enveloping, such as in the Taxaceae. It also does not include the collar of *Ginkgo* because the nature of that structure does not contribute to the micropylar region and is not understood, even after thorough developmental studies (Takaso, 1980). Although the dual vasculature of the cycad ovule has been interpreted as indicating the dual nature of the cycad "integument" (Stopes, 1905; Stevenson, 1990), because the duality is not present developmentally or in mature ovules, we have scored it as absent.

74. OUTER SEED ENVELOPE: simple (0); bi-parted (1).

Character 76 (outer seed envelope) treats the outer seed envelope when present as either simple or bifid. The bifid condition of the gnetopsids is the result of two opposite bracteoles that are fused, as demonstrated ontogenetically by Martens (1971), Takaso (1984, 1985), and Takaso & Bouman (1986).

75. MEGASPORANGIUM: w/lagenostome (0); w/pollen chamber (1); angiospermous (2); nonadditive.

This character deals with the structure of the apex (micropylar region) of the ovule, and whether the innermost (or sole) integument forms a pollen chamber. The angiospermous type lacks a pollen chamber per se.

76. INNER INTEGUMENT: not-bifid (0); bifid (1).

This character has not been used in previous seed plant analyses, but was clearly illustrated in numerous extant taxa by various workers. The bifid nature of the integument is obvious in mature ovules of certain fossil taxa but only observable during seed development in most extant gymnosperms; this may bias scores against finding bifid seeds in the fossil record. The bifid nature of the integument has been demonstrated for *Ginkgo* (Takaso, 1980) and most conifer genera (Bierhorst, 1971; Takaso, 1981; Takaso & Tomlinson, 1989a, b, 1990, 1991, 1992a, b). There is no evidence for a bifid integument in the gnetopsids (Martens, 1871; Takaso, 1984, 1985; Takaso & Bouman 1986) or angiosperms (Bouman, 1984).

77. CONE SCALE SEED WING: absent (0); present (1).

This character is included to encourage resolution within the conifers.

78. SEED COAT: simple (0); sclerotesta/sarcotesta (1).

The nature of the mature integument has been used in previous analyses in similar form. The simple seed coat has only a sclerified layer in contrast to seeds with distinct fleshy and sclerified layers.

79. INTEGUMENT VASCULATURE: single (0); double (1).

This character refers to the dual vascular system found in the seeds of medullosans and cycads (Stopes, 1905; Crane, 1988; Stevenson, 1990). The origin of this dual vasculature is believed by Stopes (1905) to have been derived from fusion of an outer seed envelope to the integument.

80. SEED CORONULA: absent (0); present (1).

The seed coronula refers to the specialized area of sclerotesta of the seed coat at the micropylar end. This is restricted to the cycad families Stangeriaceae and Zamiaceae (Stevenson, 1990).

81. NUCELLAR CUTICLE: thin (0); thick (1).

Routinely used in analyses of seed plants and the states for taxa are given in most morphology and paleobotany texts.

82. MEGASPORE TETRAD: tetrahedral (0); linear (1); isobilateral (2); nonadditive.

This character is routinely used in analyses of seed plants, and the states for taxa are given in most morphology and paleobotany texts.

83. MEGASPORE WALL: thick (0); thin/absent (1).

Widely used in previous seed plant analyses.

84. MEGAGAMETOPHYTE: monosporic (0); tetrasporic (1).

Widely used in seed plant analyses. Most fossil taxa are problematic and scored as unknown.

85. MEGAGAMETOPHYTE: alveolar (0); nonalveolar (1).

Not previously used in seed plant analyses. Data concerning the alveolar nature of the megagametophyte for extant gymnosperms are from Singh (1978) and Taylor & Taylor (1993); for some fossil taxa, data are from examination of additional published figures. Fortunately, the developmental pattern of the alveolar megagameto-

phyte is observable in mature seeds and thus is preserved in many fossils.

86. ARCHEGONIA: present (0); absent (1).

Widely used in seed plant analyses. Equivocal in many fossils due to inadequate detail of preservation.

87. EGG: cellular (0); free-nuclear (1).

Not previously used in seed plant analyses. This character is observable in mature seeds, and thus scoring is not limited to extant taxa but is also possible in those fossil taxa where archegonia have been observed (e.g., Glossopteris, Cordaites).

88. EARLY EMBRYOGENY: free-nuclear (0); cellular (1).

Data from Singh (1978) and Bierhorst (1971). Unfortunately, this character can only be scored for extant taxa because early embryo stages typically are not preserved in fossils.

89. EMBRYO MATURITY: postshed (0); preshed (1).

Not previously used in seed plant analyses. The states, postshed versus preshed, refer to the timing of embryo development. In preshed maturity, the embryo is well developed before the seed is shed from its parent plant, in contrast to postshed maturity, where the embryo development (and in some instances fertilization) occur after the seed is shed from its parent plant, as in cycads and *Ginkgo*. This character has been scored for some fossils, particularly those that have seeds with well-developed embryos known such as in *Cordaites*. In other cases, where dispersed seeds are known without embryos but well-developed megagametophytes and archegonia are present, we have inferred that embryo maturity is postshed, by analogy with living taxa such as cycads and *Ginkgo*.

90. EMBRYO FEEDER: absent (0); present (1).

This character is scored only for extant taxa and is known only in gnetopsids.

91. SEED GERMINATION: cryptocotylar (0); phanerocotylar (1).

This character is identical to that used by Loconte & Stevenson (1990). In general, cryptocotylar is equivalent to hypogeal and phanerocotylar is equivalent to epigeal germination. This character has been scored as ambiguous for fossil taxa.

92. FLORAL CUP: absent (0); present (1).

The floral cup, as a concave, usually fleshy structure bearing free appendages such as bracts (or perianth) and stamens, staminodes, and possibly carpels, is found in several magnoliid taxa such as *Calycanthus*, various Laurales, and *Eupomatia*, and may have much wider occurrence in modified form than is generally appreciated (e.g., postfertilization structures in Lauraceae). We distinguish between such apparently axial structures and the "calyx cup" of various hamamelidid, rosid, and asterid taxa, in which the contribution of the stem receptacle is either not apparent or is secondary. We have avoided use of the term "hypanthium" because it has been variously and inconsistently applied to structures formed mostly of stem receptacle or mostly of calyx and other floral appendages.

93. CALYX CUP: absent (0); present (1).

See previous character (92) for discussion.

94. PERIANTH: indeterminant/spiral (0); determinant/cyclical (1).

This character is scored as ambiguous for those taxa without perianth.

95. TRIMEROUS ANDROECIUM: absent (0); present (1).

This character is coded as present when one or more cycles of the androecium are in threes or even multiples thereof.

96. STAMEN FORM: filamentous (0); laminar (1).

This character is the traditional distinction between fleshy, laminar stamens and thinner, terete filamentous stamens.

97. STAMEN CONNECTIVE: absent (0); well developed (1).

The occurrence of a well-developed stamen connective, sometimes modified in various manners, is typical of many of the taxa to be considered basal in the angiosperms (Cronquist, 1981).

98. CARPEL ARRANGEMENT: spiral (0); whorled/opposite (1).

Flowers with single carpels have been coded as inapplicable for this character. Data from standard taxonomic texts and herbarium observation.

99. CARPEL NUMBER: 1 (0); 2 (1); 3 (2); 4/5 (3); nonadditive.

Scored only for those taxa with stabilized numbers of carpels (character 100).

100. CARPEL NUMBER: indeterminant (0); determinant (1).

Indeterminant carpel refers to spirals or whorls that are not fixed on particular modal numbers.

101. OVARY: apocarpous (0); syncarpous (1); syncarpous-inferior (2); additive.

This character is treated as additive because syncarpy is a prerequisite for an inferior ovary (in the sense used here). Taxa such as *Calycanthus* have an apocarpous gynoecium but are perigynous and are scored as having a floral cup, not a syncarpous inferior ovary. In all taxa in our analyses scored as syncarpous-inferior, the calyx and/or other floral appendages are clearly adnate to a syncarpous ovary.

102. PLACENTATION: marginal/laminar (0); apical (1); basal (2); nonadditive.

This character is not related to number of ovules; thus, two ovules may be apical or marginal, but in the taxa we included, taxa with numerous ovules were always state 0. This would not be the case if more angiosperm taxa were included.